

The Invertebrate Cave Fauna of Virginia

John R. Holsinger

Department of Biological Sciences
Old Dominion University
Norfolk, Virginia 23529

David C. Culver

Department of Environmental Science
American University
4400 Massachusetts Avenue NW
Washington, DC 20016

David A. Hubbard, Jr.

Virginia Speleological Survey
40 Woodlake Drive
Charlottesville, Virginia 22901

William D. Orndorff

Virginia Department of Conservation and Recreation
Division of Natural Heritage Karst Program
8 Radford Street, Suite 102
Christiansburg, Virginia 24073

Christopher S. Hobson

Virginia Department of Conservation and Recreation
Division of Natural Heritage
600 East Main Street, 24th Floor
Richmond, Virginia 23219

ABSTRACT

The obligate cave-dwelling invertebrate fauna of Virginia is reviewed, with the taxonomic status and distribution of each species and subspecies summarized. There are a total of 121 terrestrial (troglomorphic) and 47 aquatic (stygobiotic) species and subspecies, to which can be added 17 stygobiotic species known from Coastal Plain and Piedmont non-cave groundwater habitats, and published elsewhere (Culver et al., 2012a). Richest terrestrial groups are Coleoptera, Collembola, and Diplopoda. The richest aquatic group is Amphipoda. A number of undescribed species are known and the facultative cave-dwelling species are yet to be summarized.

Key words: Appalachians, biogeography, biospeleology, caves, springs, stygobionts, subterranean, troglomorphic.

INTRODUCTION

The cave fauna of Virginia, most particularly the obligate cave-dwelling fauna, has been studied and described for over 100 years. The first obligate cave-dwelling species described from a Virginia cave was a beetle, *Pseudanophthalmus pusio*, described by Horn in 1868. As of 2012, 168 obligate subterranean species have been described from Virginia caves and associated habitats (Table 1), and another 17 species described from other subterranean habitats (Culver et al., 2012a).

The present study grew out of the realization that the last compilation of the Virginia cave fauna by Holsinger & Culver (1988) was seriously out of date, and that in the intervening years extensive collections had been made in Virginia caves, especially by David Hubbard, and that many new species have been described, especially by William Shear and Kenneth Christiansen. In addition, the establishment of the Virginia Natural Heritage Program in 1986, and its extensive records of subterranean fauna, meant that it would be relatively easy to assemble information on the subterranean fauna of Virginia. Early on, we recognized that the subterranean fauna of seepage springs and shallow wells of the Coastal Plain and Piedmont, while sharing many morphological features with cave-dwelling species, especially loss of eyes and pigment and elongation of appendages (see Culver et al., 2010), was geographically distinct, and thus best treated separately. This shallow subterranean fauna, together with that of Maryland and the District of Columbia, was summarized in a separate publication (Culver et al., 2012a).

The present study enumerates the described obligate subterranean fauna of caves and associated habitats in Virginia, together with a list of all known localities, a distribution map, and some comments on the systematic status of the species and subspecies.

Table 1. Number of described troglobionts and stygobionts known from Virginia at various times. The number in parentheses is the additional number of stygobionts known from shallow subterranean habitats in the Coastal Plain and Piedmont (Culver et al., 2012a).

Reference	Troglobionts	Stygobionts
Packard (1888)	9	0
Holsinger (1963)	38	7
Holsinger & Culver (1988)	67	35
Present study	121	47(17)

METHODS AND MATERIALS

We assembled all published records, all records from the Virginia Natural Heritage Program database, and supplemented this with our own unpublished records. The final list was reconciled with the Virginia Natural Heritage Program database. All records are based on voucher specimens deposited in various museums and research collections around the world. No unconfirmed sight records are included. Locations were obtained from the same sources, and supplemented by information supplied by the Virginia Speleological Survey. In a very few cases, especially old records involving springs, it was not possible to determine an exact location. All locations have an error of less than 1 km. Distribution maps were created using ArcMap 10. In order to emphasize not only where a species was found but also where it was not found, gray dots on all maps indicate all terrestrial or aquatic sampling sites, depending on the species. A map of the counties where caves were sampled is shown in Fig. 1.

The most difficult decision was selecting which species to include in this review. Holsinger & Culver (1988) treated both obligate and non-obligate cave-dwelling species, including both described and undescribed species. We decided to include only described, obligate cave-dwelling species in this paper for several reasons. The first is a practical one—the number of species has grown to such an extent that even the limitation to described obligate cave-dwellers is a formidable one. Second, records on species that are not obligate cave-dwellers are very incomplete, and very few new records have been added since the Holsinger & Culver report. This is not to imply that these species are unimportant. Many are major components of both aquatic and terrestrial communities, and in the case of crickets (the genera *Ceuthophilus* and *Euhadenocercus*), they are a major source of organic carbon and nutrients as a result of their regular trips in and out of caves. The third reason has to do with limitation to described species. Undescribed species range from ones that have been well studied, with detailed drawings, but are not yet published to those that are not adequately characterized or described. Even in the case of the cave fauna where endemism is the rule, not all potential undescribed species turn out to be new species upon further study. About one-third, on closer examination, prove to be minor variants of existing species (Culver et al., 2012b).

Our criterion for inclusion of a described species in this list is that at least 90 percent of the records for the species were from subterranean habitats. This distributional definition corresponds to the original

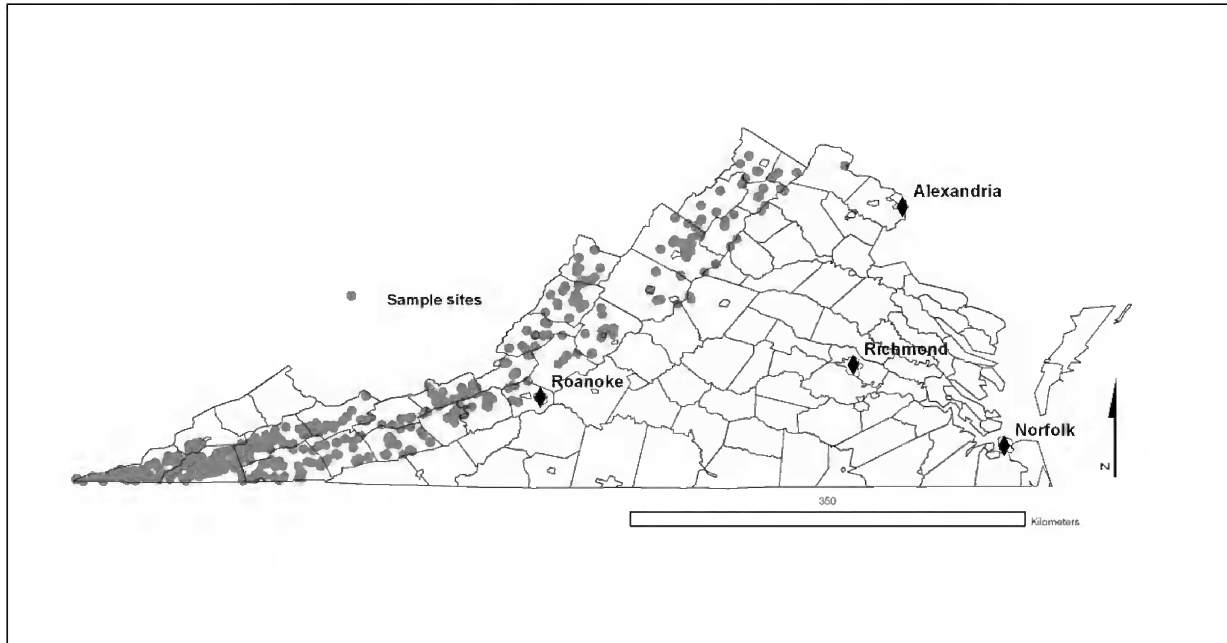


Fig. 1. Distribution of sampling sites in Virginia. More than 95 percent of these records are from caves; the rest are from springs and other groundwater-associated habitats.

ecological classification of Schiner (1854) and others (see Sket, 2008), with troglobionts (terrestrial) and stygobionts (aquatic) the terms for obligate subterranean dwellers. Most troglobionts and stygobionts have reduced or absent eyes and pigment, and these criteria (collectively termed troglomorphy by Christiansen [1962]) have sometimes been used to determine which species are troglobionts and stygobionts. Operationally, this often works but there are several problems. First, it is often difficult to determine how much eye and pigment reduction is necessary to call a species troglomorphic. Second, troglomorphy is based on the idea of strong convergence of subterranean species, but this is being challenged by the discovery of divergence of stygobionts and troglobionts within a community (Fišer et al., 2012). Pipan & Culver (2012) point out that most cave communities have non-troglomorphic species, and that many other subterranean habitats have troglomorphic species. As Daniel Fong (pers. comm.) points out, troglomorphy is a hypothesis, not an invariant law. In those cases where non-troglomorphic species have been included, we have indicated such. It may well be that some or most of these species will prove to be troglophiles and stygophiles rather than

troglobionts and stygobionts, but until they have been regularly found outside of caves, we have included them.

RESULTS

A total of 121 troglomorphic and 47 stygobiotic species and subspecies have been found in Virginia caves. In 1988, the comparable numbers were 67 and 35 (Table 1). Comparable numbers are not available for most states, but in neighboring West Virginia there are 63 troglobionts and 33 stygobionts (updated from Fong et al., 2007). In Arkansas, there are 27 troglobionts and 28 stygobionts (Graening et al., 2011).

The taxonomic distribution of the troglobionts and stygobionts is enumerated in Table 2. Among stygobionts, amphipods with 51 percent (24) of the species and subspecies, are the most diverse. The only other order with more than ten percent of the known stygobionts is Isopoda, with 13 species. Three orders dominate the terrestrial fauna, each with 23 or more species — chordeumatid millipeds, Collembola, and Coleoptera (Table 2). Only one other order, Pseudoscorpiones with 13 species, has as much as 10 percent of the fauna.

Table 2. Taxonomic position of Virginia stygobionts and troglobionts, excluding species from the Piedmont and Coastal Plain.

Phylum	Class	Order	Number of Aquatic Species and Subspecies	Number of Terrestrial Species and Subspecies
Platyhelminthes	Turbellaria	Lecithoepetheliata	1	
		Tricladida	3	
Annelida	Clitellata	Lumbriculida	2	
Mollusca	Gastropoda	Mesogastropoda	4	
Arthropoda	Chelicerata	Acari		4
		Araneae		10
		Pseudoscorpiones		13
	Diplopoda	Chordeumatida		23
	Chilopoda	Lithobiomorpha		1
	Hexapoda	Collembola		29
		Diplura		4
	Insecta	Coleoptera		32
		Diptera		1
	Malacostraca	Amphipoda	24	
		Isopoda	13	4

ANNOTATED LIST OF SPECIES

PHYLUM PLATYHELMINTHES

Class Turbellaria

Order Lecithoepetheliata

Family Prorhynchidae

Geocentrophora cavernicola Carpenter 1970

Type Locality: John Rogers Cave, Jackson County, Kentucky

Virginia Record (Fig. 2): **Tazewell Co.**: Fallen Rock Cave.

Remarks: This is the only species in the genus known from subterranean sites in North America. However, two other species of *Geocentrophora* are recorded from subterranean waters in Europe (Schwank, 1986). *G. cavernicola* is also known from Blowhole Cave, Pendleton Co., West Virginia (Fong et al., 2007).

Order Tricladida

Family Kenkiidae

Sphalloplana chandleri Kenk 1977

Type Locality: Stokes Lane spring, Davidson County, Tennessee

Virginia Record (Fig. 3): **Tazewell Co.**: Fallen Rock Cave.

Remarks: This planarian is also known from a cave spring in Tennessee, as well as a spring in Floyd Co., Indiana. The type locality spring issues from a cave (Kenk, 1977).

Sphalloplana consimilis Kenk 1977

Type Locality: Gallohan No. 1 Cave, Lee County, Virginia

Other Virginia Records (Fig. 3): **Lee Co.**: Bowling Cave, Cope Cave, Gregorys Cave, Hamblin School Cave, McClure Cave.

Remarks: The occurrence of this species is sporadic but it is common where found. It is also known from Claiborne County, Tennessee, and is endemic to the Powell River watershed in Virginia and Tennessee.

Sphalloplana virginiana Hyman 1945

Type Locality: Showalter Cave, Rockbridge County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 3).

Remarks: The species is apparently endemic to a single cave. Holsinger & Culver (1988) noted that previous records from Bland and Lee counties (Holsinger, 1963) are invalid in light of subsequent revisionary studies by Kenk (1977).

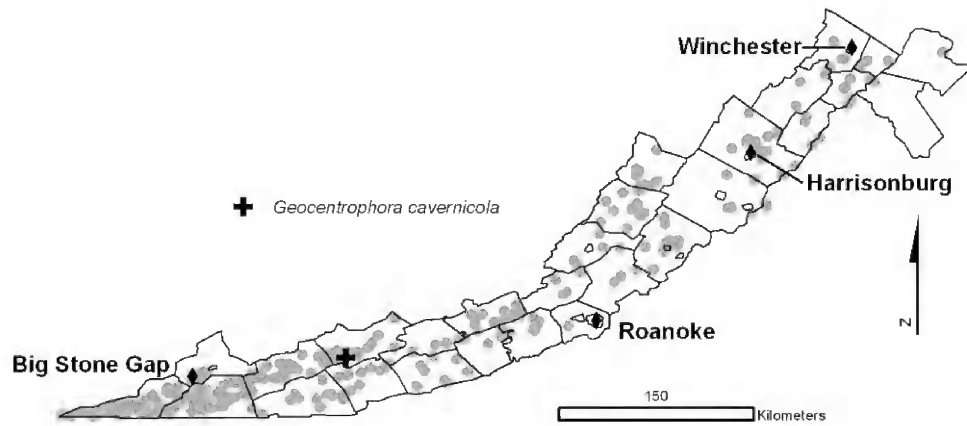


Fig. 2. Distribution of *Geocentrophora cavernicola* in Virginia. Gray dots are all the aquatic sampling sites.

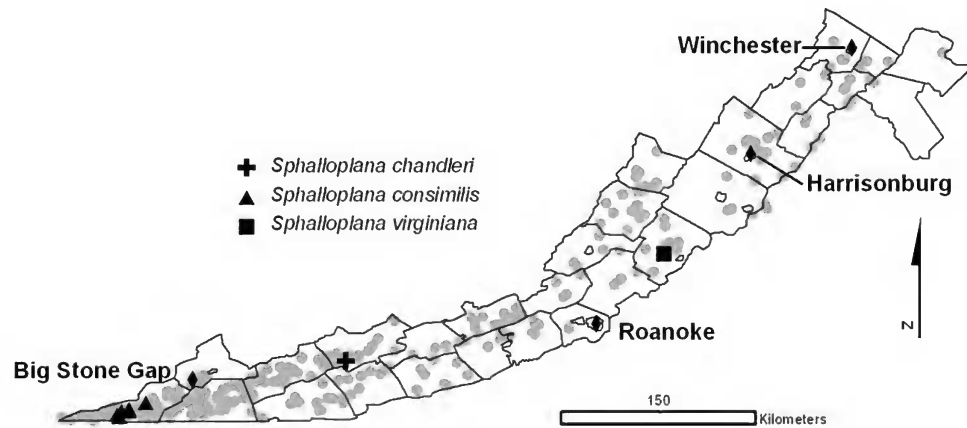


Fig. 3. Distribution of *Sphalloplana chandleri*, *S. consimilis*, and *S. virginiana* in Virginia. Gray dots are all the aquatic sampling sites.

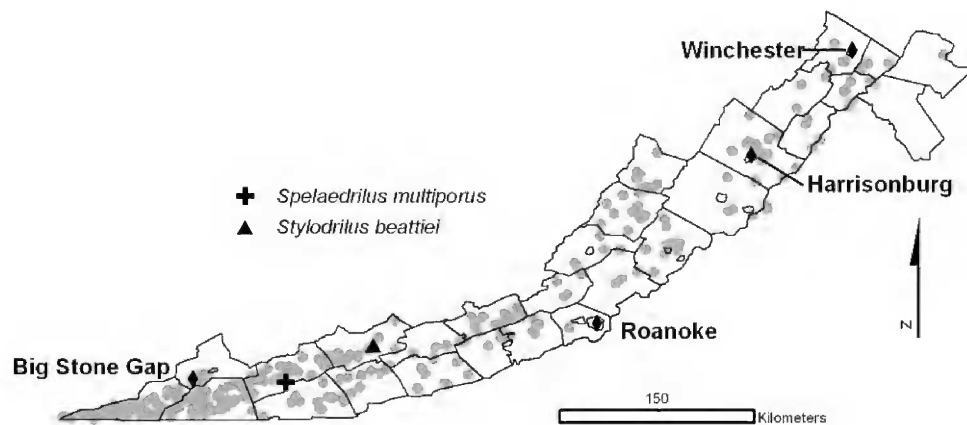


Fig. 4. Distribution of *Spelaedrillus multiporus* and *Stylo-drilus beattiei* in Virginia. Gray dots are all the aquatic sampling sites.

PHYLUM ANNELIDA**Class Clitellata****Order Lumbriculida****Family Lumbriculidae**

Spelaedrillus multiporus Cook 1975

Type Locality: Smiths Cave, Russell County, Virginia
Other Virginia Records: Known only from the type locality (Fig. 4).

Remarks: This is the only species in the genus.

Stylodrilus beattiei Cook 1975

Type Locality: Tub Cave, Pocahontas County, West Virginia

Virginia Record (Fig. 4): **Tazewell Co.**: Steeles Cave.

Remarks: This worm is also known from Court Street Cave and Friars Hole Cave in Greenbrier Co., West Virginia (Fong et al., 2007).

PHYLUM MOLLUSCA**Class Gastropoda****Order Mesogastropoda****Family Hydrobiidae**

Fontigens bottimeri (Walker 1925)

Type Locality: Glenn Echo, Montgomery County, Maryland

Virginia Records (Fig. 5): **Frederick Co.**: Ogdens Cave, seep 0.8 km S of Hayfield.

Remarks: Found in both caves and small springs in the Potomac and Shenandoah River basins in northern Virginia, Maryland, and District of Columbia (Hershler et al., 1990), this snail is listed as a State Endangered Species in Virginia. Its distribution in the rest of the state is shown in Culver et al. (2012a). It ranges in size from 1 to 3 mm.

Fontigens morrisoni Hershler, Holsinger & Hubricht 1990

Type Locality: A small, spring-fed brook SW of Mustoe, Highland County, Virginia

Other Virginia Records (Fig. 5): **Bath Co.**: Blowing Cave; **Highland Co.**: Aqua Cave, Butler-Sinking Creek Cave, Vandevander Cave, spring 2.1 km N of Mustoe.

Remarks: A small species (1.5-2.5 mm) that can be found in both springs and cave habitats within the upper James River watershed.

Fontigens tartarea Hubricht 1963

Type Locality: Organ Cave, Greenbrier County, West Virginia

Virginia Records (Fig. 5): **Bath Co.**: Crossroads Cave; **Highland Co.**: Secret Anthodite Cave.

Remarks: One of the smallest freshwater snails (1.7-2 mm) in eastern North America, it was discovered in Virginia for the first time in 1994.

Holsingeria unthinksensis Hershler 1989

Type Locality: Unthanks Cave, Lee County, Virginia

Other Virginia Records (Fig. 5): **Lee Co.**: Burial Cave, Gibson No. 1 Cave, Jones Saltpetre Cave, Tater Cave.

Remarks: This local endemic is found among small submerged rocks in small streams in five caves confined to a portion of the Powell River basin in Lee County, Virginia. It is listed as a State Endangered Species.

PHYLUM ARTHROPODA**Class Chelicerata****Order Acari****Family Rhagidiidae**

Poecilophysis extraneostella Zacharda 1985

Type Locality: Bowling Cave, Lee County, Virginia

Other Virginia Records: Known in Virginia only from the type locality (Fig. 6).

Remarks: Although this mite is known only from caves and hence by definition is a troglobiont, it shows little if any modification for subterranean life. It is also known from four caves in West Virginia (Fong et al., 2007).

Poecilophysis weyerensis (Packard 1888)

Type Locality: Grand Caverns, Augusta County, Virginia

Other Virginia Record (Fig. 6): **Rockbridge Co.**: Buck Hill Cave.

Remarks: Originally described by Packard (1888) from Grand Caverns, it was redescribed by Holsinger (1965) and subsequently reported from caves in Missouri, New Mexico, and Mexico by Elliott & Strandtmann (1971). Zacharda (1980) listed this species (synonym = *Rhagidia cavernarum*) from Long Cave in Edmonson County, Kentucky, and from scree habitats in the Czech Republic, but questioned the records given by Elliott & Strandtmann (1971). Zacharda (1985) gave an additional record from Buck Hill Cave as well as Sensabaugh Saltpetre Cave in Hawkins Co., Tennessee. As with *P. extraneostella*, it shows little

morphological modification for cave life.

Rhagidia varia Zacharda 1985

Type Locality: Butler-Sinking Creek Cave, Bath County, Virginia

Other Virginia Records (Fig. 6): **Bath Co.**: Starr Chapel Disappointment Cave; **Scott Co.**: Hill Cave; **Wythe Co.**: Sam Six Cave.

Remarks: This predaceous mite is often found in leaf litter in caves. It presumably preys upon other mites and especially Collembola. It is also known from caves in West Virginia (Zacharda, 1985).

Traegardhia parallelseta (Zacharda 1985)

Type Locality: Sam Six Cave, Wythe County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 6).

Remarks: According to Zacharda et al. (2010), *T. parallelseta* shows extensive morphological modification for cave life, such as elaborated sensory structures (solenidia) on the tibia and elsewhere. It is known from one specimen!

Order Araneae

Family Linyphiidae

Anthobia coylei Miller 2005a

Type Locality: Benedicts Cave, Greenbrier County, West Virginia

Virginia Records (Fig. 7): **Alleghany Co.**: Wares Cave; **Bath Co.**: Clarks Cave.

Remarks: Formerly assigned to *A. monmouthia*, Miller (2005a) recognized these records and a number of additional records from Greenbrier, Mercer, Monroe, and Pocahontas counties in West Virginia (Fong et al., 2007) as being a distinct species.

Anthobia monmouthia Tellkamp 1844

Type Locality: Mammoth Cave, Edmonson County, Kentucky

Virginia Records (Fig. 7): **Scott Co.**: Harris Pit Cave, McNew Cave; **Smyth Co.**: Buchanan Saltpetre Cave.

Remarks: This widespread troglomorphic spider is also found in many caves in Kentucky and Tennessee.

Bathypantes weyeri (Emerton 1875)

Type Locality: Grand Caverns, Augusta County, Virginia

Other Virginia Records: Known in Virginia only from the type locality (Fig. 7).

Remarks: This species is widely distributed in caves

from Wisconsin and Arkansas east to Pennsylvania, Virginia, and West Virginia (Ivie, 1969), but it is found in relatively few caves in any region. Paquin & Dup  r   (2003) report this species from surface localities in Canada. It may be that the species is troglomorphic in southern parts of its range, such as Virginia, and troglophilic in northern parts of its range, but this conjecture needs further field studies for confirmation. As with other Linyphiidae, it is a predator, probably of mites and Collembola.

Islandiana muma Ivie 1965

Type Locality: Buck Hill Cave, Rockbridge County, Virginia

Other Virginia Records: Known in Virginia only from the type locality (Fig. 7).

Remarks: This is a very rare species with an enigmatic distribution. In addition to the type locality, it is only known from one cave in Colbert County, Alabama (Ivie, 1965).

Oreonetides beattyi Paquin, Dup  r  , Buckle & Lewis 2009

Type Locality: Smiths Folly Cave, Lawrence County, Indiana

Virginia Records (Fig. 7): **Montgomery Co.**: Vicker Road Cave; **Tazewell Co.**: Rosenbaums Water Cave.

Remarks: This species is also known from caves in Indiana, Maryland, Pennsylvania, and Tennessee. There is variation in the amount of eye reduction, but it is reduced in all populations (Paquin et al., 2009).

Phanetta subterranea (Emerton 1875)

Type Locality: Wyandotte Cave, Crawford Co., Indiana
Virginia Records (Fig. 8): **Alleghany Co.**: Blue Spring Cave, Fudges Cave, Island Ford Cave, Lowmoor Cave, Wares Cave; **Augusta Co.**: Fountain Cave, Madison Saltpetre Cave; **Bath Co.**: Boundless Cave, Breathing Cave, Butler-Sinking Creek Cave, Cave Run Pit Cave, Clarks Cave, Dunns Cave, Russells Reserve Cave, Starr Chapel Saltpetre Cave; **Bland Co.**: Hamilton Cave; **Botetourt Co.**: Peerys Saltpetre Cave, Thomas Cave; **Craig Co.**: Rufe Caldwell Cave; **Frederick Co.**: Ogdens Cave; **Giles Co.**: Clover Hollow Cave, Giant Caverns Cave, Harris Cave, New River Cave, Salamander Cave, Smokehole Cave, Starnes Cave, Straleys No. 1 Cave, Tawneys Cave; **Highland Co.**: Vandevander Cave; **Lee Co.**: Bowling Cave, Cudjo's Cavern (part of the Gap Cave System), Cumberland Gap Saltpetre Cave (part of the Gap Cave System), Gibson-Frazier Cave, Lucy Beatty Cave, Molly Wagle Cave, Olinger Cave, Spangler Cave; **Montgomery Co.**: Slussers Chapel Cave; **Page Co.**: Luray Caverns;

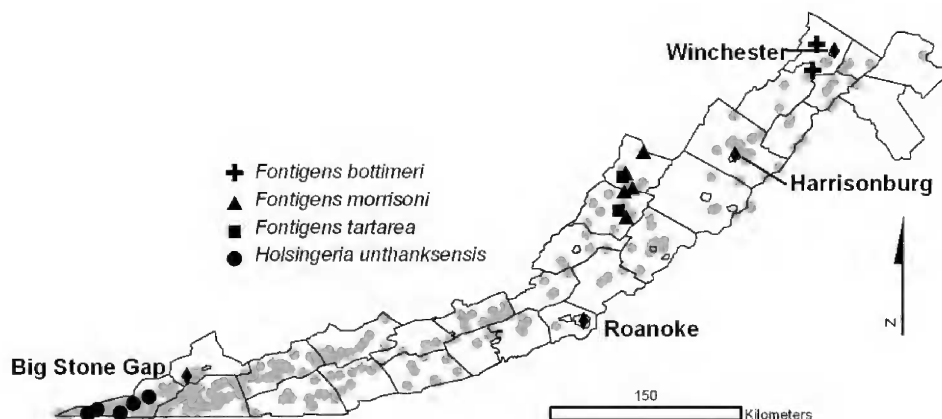


Fig. 5. Distribution of *Fontigens bottimeri*, *F. morrisoni*, *F. tartarea*, and *Holsingeria unthinksensis* in Virginia. Gray dots are all the aquatic sampling sites.

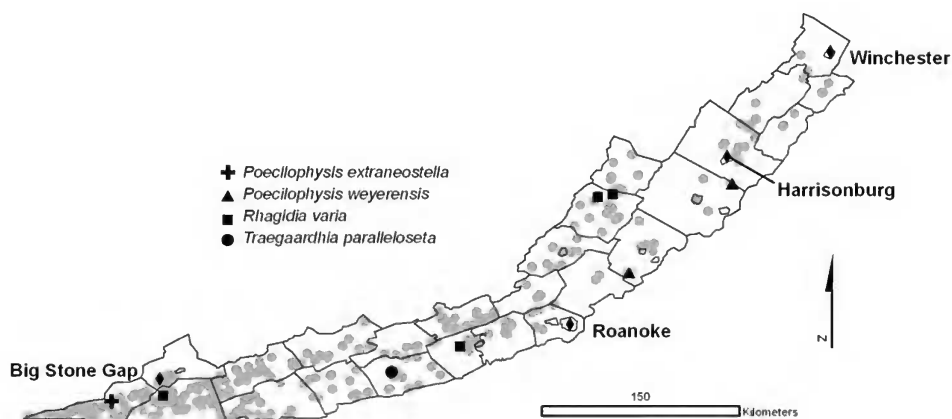


Fig. 6. Distribution of *Poecilophysis extraneostella*, *P. weyerensis*, *Rhagidia varia*, and *Traegardhia paralleloseta* in Virginia. Gray dots are all the terrestrial sampling sites.

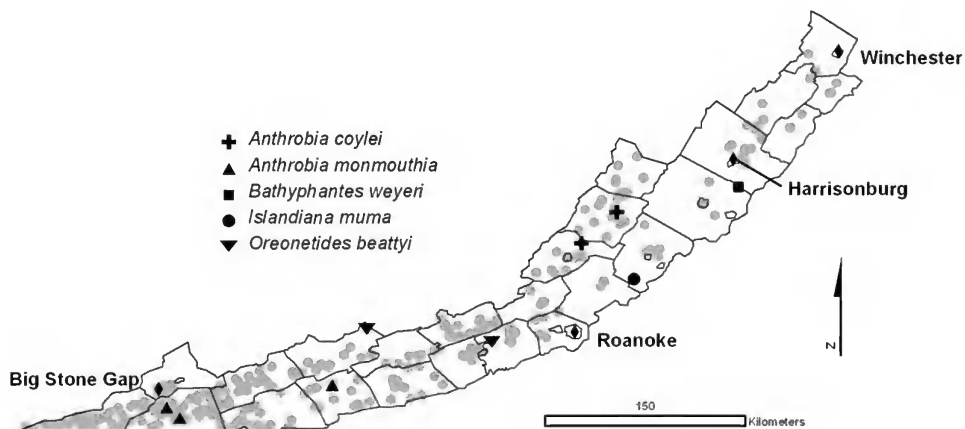


Fig. 7. Distribution of *Anthrobia coylei*, *A. monmouthia*, *Bathyphantes weyeri*, *Islandiana muma*, and *Oreonetides beattyi* in Virginia. Gray dots are all the terrestrial sampling sites.

Pulaski Co.: Sam Bells Cave; **Roanoke Co.:** Goodwins Cave, Hodges No. 1 Cave, Millers Cove Cave; **Rockingham Co.:** Deer Drop Cave; Massanutten Caverns; Melrose Caverns, Stephens Cave; **Russell Co.:** Banners Corner Cave, Concrete Tank Cave, Daugherty Cave, Densmore Hill Cave, Dorton Spring Cave, Echo Lake Cave, Jessie Cave, Litton Cave, Mountain View Cave, Porgie Bundys Cave, Stewart Monks Cave, Tumbez Cave; **Scott Co.:** Carlinbrook Cave, Cave Hollow Cave, Grigsby Cave, Herron No. 1 Cave, Hill Cave, Jesse Branch Cave, Kerns No. 1 Cave, Sounding Cave, Valley Creek Pirate Cave, Winding Stair Cave; **Smyth Co.:** Beaver Creek Cave; **Tazewell Co.:** Cassell Farm Cave No. 2, Chimney Rock Cave, Higginbotham No. 1 Cave, Lawson Cave, Steeles Cave; **Warren Co.:** Skyline Caverns; **Washington Co.:** Hall Bottom No. 1 Cave, Perkins Cave, Red Wolf Cave; **Wise Co.:** Kelly Cave, Wildcat Saltpetre Cave; **Wythe Co.:** Picketts Cave.

Remarks: This is the most common and widespread troglomorphic spider in Virginia caves. It is also common in caves throughout the eastern United States and ranges from Pennsylvania south to Georgia and Alabama and west to Missouri and Illinois.

Porrhomma cavernicola (Keyserling 1886)

Type Locality: Reynolds Cave, Barren County, Kentucky

Virginia Records (Fig. 9): **Augusta Co.:** Fountain Cave, Glade Cave, Madison Saltpetre Cave; **Bath Co.:** Clarks Cave, Crossroads Cave, Porters Cave, Witheros Cave; **Bland Co.:** Banes Spring Cave, Coon Cave; **Craig Co.:** New Castle Murder Hole, Rufe Caldwell Cave; **Frederick Co.:** Beans Cave; **Giles Co.:** Clover Hollow Cave; **Lee Co.:** Fisher Cave, Unthanks Cave; **Montgomery Co.:** Aunt Nellies Hole Cave; **Page Co.:** Luray Caverns, Ruffners No. 1 Cave; **Roanoke Co.:** Dixie Caverns; **Rockbridge Co.:** Bell Cave, Rock Hill Cave; **Rockingham Co.:** 3-D Maze Cave; **Russell Co.:** Cartop Cave, Maggie Baker Cave; **Scott Co.:** Abrams Cave, Little Duck Cave, Queens Cave; **Smyth Co.:** Buchanan Saltpetre Cave; **Tazewell Co.:** Gully Cave, Lawson Cave; **Washington Co.:** Robinson Cave; **Wise Co.:** Parsons Cave; **Wythe Co.:** Sam Six Cave.

Remarks: This species, like *P. subterranea*, occurs over much of the eastern United States. It ranges from Pennsylvania south to Georgia and west to Missouri and Oklahoma. These two species have among the largest ranges of any North American troglomorphic or stygobiont. This large range would seem to indicate that it is either a species complex or is not really a troglomorphic, and thus able to disperse through and survive in surface habitats. However, it is practically

unknown from surface habitats and Miller (2005b) found no morphological differences among populations in different parts of its range. It is possible that this taxon may encompass cryptic species detectable only from DNA sequencing.

Family Nesticidae

Nesticus holsingeri Gertsch 1984

Type Locality: Pond Cave, Scott County, Virginia

Other Virginia Records (Fig. 10): **Lee Co.:** Bowling Cave, Gibson No. 1 Cave; **Montgomery Co.:** Eve Einstein Cave; **Pulaski Co.:** Collier Cave; **Russell Co.:** Austins Hilltop Cave, Carpenters Cave, Concrete Tank Cave, Ferguson Cave, Stewart Monks Cave; **Scott Co.:** Alley Cave, Blair-Collins Cave, Coley No. 2 Cave, Jackson Cave, McDavids Cave, Pond Cave, Taylor No. 1 Cave; **Washington Co.:** Thomas No. 1 Cave; **Wise Co.:** Burton Cave.

Remarks: This species is known only from caves in southwestern Virginia. Eyes are present but reduced.

Nesticus paynei Gertsch 1984

Type Locality: Reeder's Cave, Anderson County, Tennessee

Virginia Record (Fig. 11): **Scott Co.:** Wolfe Cave.

Remarks: This species is common in caves in eastern Tennessee. Although it has well developed eyes, it is known only from caves (Gertsch, 1984).

Nesticus tennesseensis (Petrunkevitch 1925)

Type Locality: Indian Cave, Grainger County, Tennessee

Virginia Records (Fig. 11): **Alleghany Co.:** Rumbolds Cave; **Craig Co.:** Fish Hatchery Cave, Walkthrough Cave; **Giles Co.:** Ballards Cave, Doe Mountain Cave, Giant Caverns Cave, Glenlyn Cave, Harris Cave, Starnes Cave, Straleys No. 1 Cave, Sugar Run Cave System; **Highland Co.:** Locust Cave; **Lee Co.:** Cattle Cave; **Russell Co.:** Broken Formation Cave, Dorton Spring Cave; **Scott Co.:** Booher Cave; **Smyth Co.:** Sugar Grove No. 10 Cave; **Tazewell Co.:** Cassell Farm No. 2 Cave, Chimney Rock Cave, Fallen Rock Cave, Hugh Young Cave, Steeles Cave; **Wise Co.:** Hairy Hole Cave.

Remarks: In addition to the localities listed above, this species is known from caves in West Virginia and Tennessee. According to Gertsch (1984), it is morphologically variable and is sometimes found in surface habitats in Virginia and West Virginia, but not in Tennessee. However, nearly all records are from caves and therefore we consider it a troglomorphic. It shows variable amounts of eye and pigment reduction.

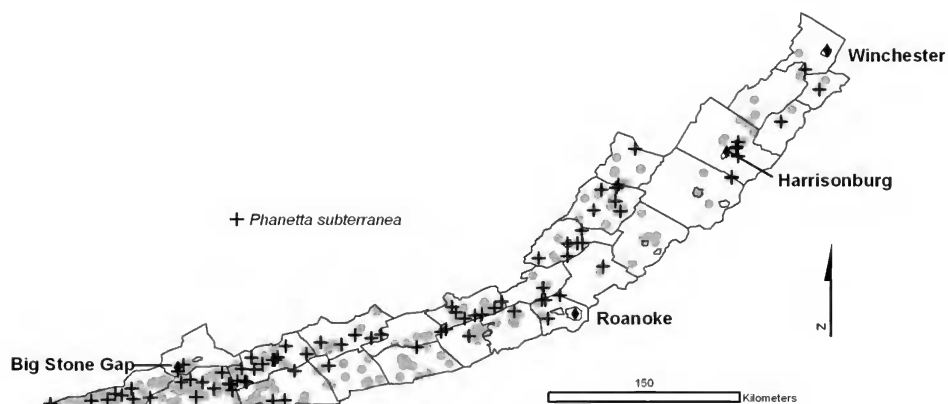


Fig. 8. Distribution of *Phanetta subterranea* in Virginia. Gray dots are all the terrestrial sampling sites.

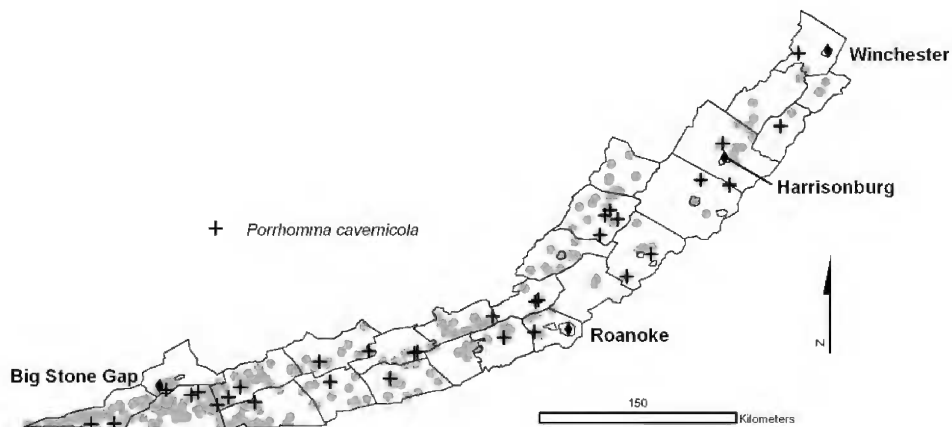


Fig. 9. Distribution of *Porrhomma cavernicola* in Virginia. Gray dots are all the terrestrial sampling sites.

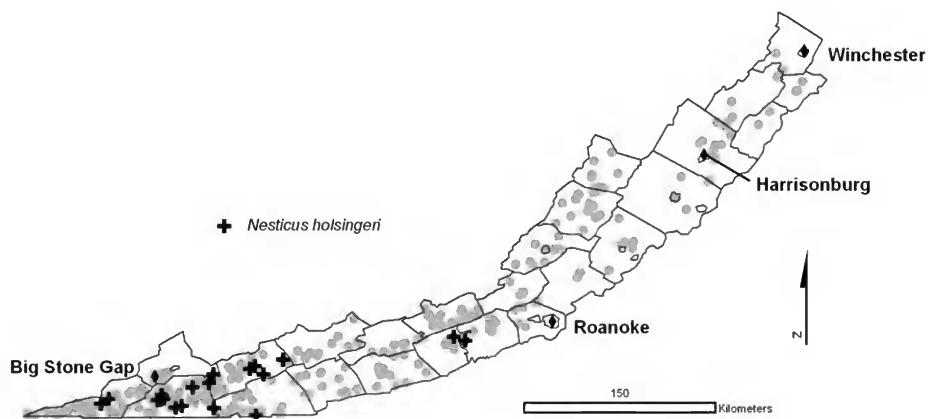


Fig. 10. Distribution of *Nesticus holsingeri* in Virginia. Gray dots are all the terrestrial sampling sites.

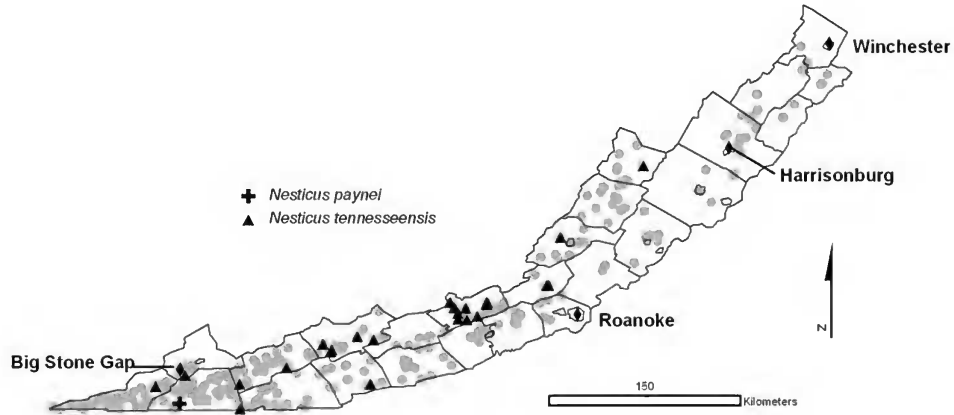


Fig. 11. Distribution of *Nesticus paynei* and *N. tennesseensis* in Virginia. Gray dots are all the terrestrial sampling sites.

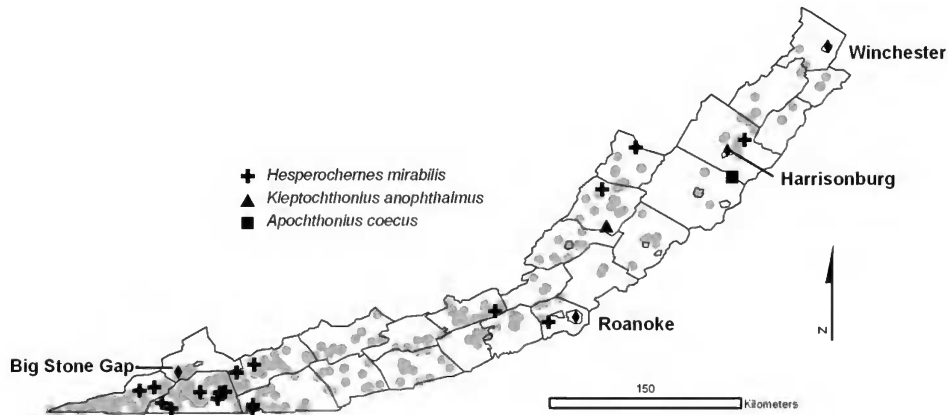


Fig. 12. Distribution of *Apochthonius coecus*, *Hesperocheernes mirabilis*, and *Kleptochthonius anophthalmus* in Virginia. Gray dots are all the terrestrial sampling sites.

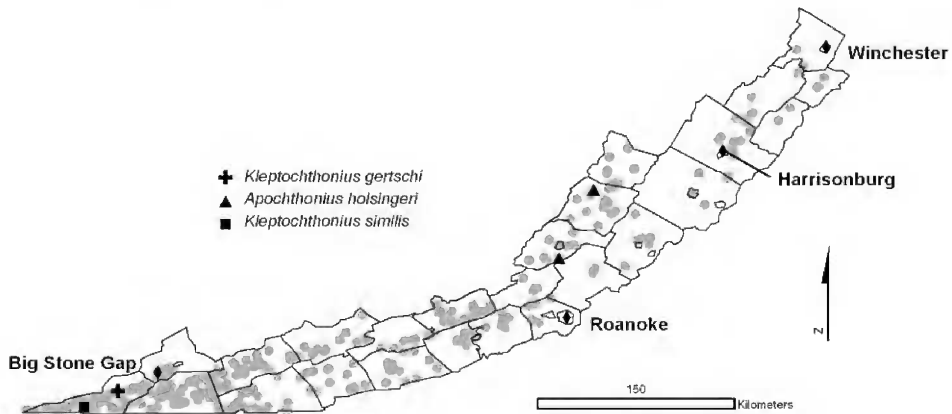


Fig. 13. Distribution of *Apochthonius holsingeri*, *Kleptochthonius gertschi*, and *K. similis* in Virginia. Gray dots are all the terrestrial sampling sites.

Order Pseudoscorpiones

Family Chernetidae

Hesperochernes mirabilis (Banks 1895)

Type Locality: "Cave at Pennington Gap", Lee County, Virginia

Other Virginia Records (Fig. 12): **Bath Co.:** Cave Run Pit Cave; **Giles Co.:** Smokehole Cave; **Highland Co.:** Vandevander Cave; **Lee Co.:** Gilley Cave, Secret Cave; **Roanoke Co.:** Goodwins Cave; **Rockingham Co.:** Eggleston Cave; **Russell Co.:** Boy Scout Cave, Ferguson Hollow Cave; **Scott Co.:** Basil Duncan Cave, Big Spiders in a Little Maze Cave, Canyon to Nowhere Cave, Creek No. 1 Cave, Darty Cave, McCulley Cave, W.R. Combs Cave; **Washington Co.:** Davenport Cave, Three Chambers Cave.

Remarks: This species is also known from caves throughout the southeastern U.S. (Holsinger & Culver, 1988; Niemiller & Zigler, 2013). It appears to be morphologically unmodified for subterranean life, but it has not been found outside of caves.

Family Chthoniidae

Apochthonius coecus (Packard 1884)

Type Locality: Grand Caverns, Augusta County, Virginia

Other Virginia Record (Fig. 12): **Augusta Co.:** Madison Saltpetre Cave.

Remarks: Chthoniidae, including all the species listed below, are typically found in damp places, under rocks or wood.

Apochthonius holsingeri Muchmore 1967

Type Locality: Cave Run Pit Cave, Bath County, Virginia

Other Virginia Record (Fig. 13): **Alleghany Co.:** Blue Spring Cave.

Kleptochthonius anophthalmus Muchmore 1970

Type Locality: Porters Cave, Bath County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 12).

Kleptochthonius binoculatus Muchmore 1974

Type Locality: Hill Cave, Scott County, Virginia

Other Virginia Records (Fig. 14): **Scott Co.:** Dancing Rock Cave, Jack Hartstock Cave, Jimmys Suck Hole Cave.

Remarks: For a pseudoscorpion, it has a large distribution, being known from four caves!

Kleptochthonius gertschi Malcolm & Chamberlin 1961

Type Locality: Gilley Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 13).

Kleptochthonius lutzi Malcolm & Chamberlin 1961

Type Locality: Cudjo's Cavern (part of the Gap Cave System), Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 14).

Kleptochthonius proximisetus Muchmore 1976

Type Locality: Gallohan No. 1 Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 15).

Kleptochthonius regulus Muchmore 1970

Type Locality: Fallen Rock Cave, Tazewell County, Virginia

Other Virginia Record (Fig. 15): **Tazewell Co.:** Higginbotham No. 1 Cave.

Kleptochthonius similis Muchmore 1976

Type Locality: Sweet Potato Cave, Tazewell County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 13).

Mundochthonius holsingeri Benedict & Malcolm 1974

Type Locality: Helsley Cave, Shenandoah County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 14).

Family Neobisiidae

Lissocreagris valentinei (Chamberlin 1962)

Type Locality: Cudjo's Cavern (part of the Gap Cave System), Lee County, Virginia

Other Virginia Record (Fig. 15): **Lee Co.:** Indian Cave.

Family Syanaridae

Chitrella superba Muchmore 1973

Type Locality: Maddens Cave, Shenandoah County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 15).

Remarks: This rare species is less morphologically modified than most of the species in the family Chthoniidae.

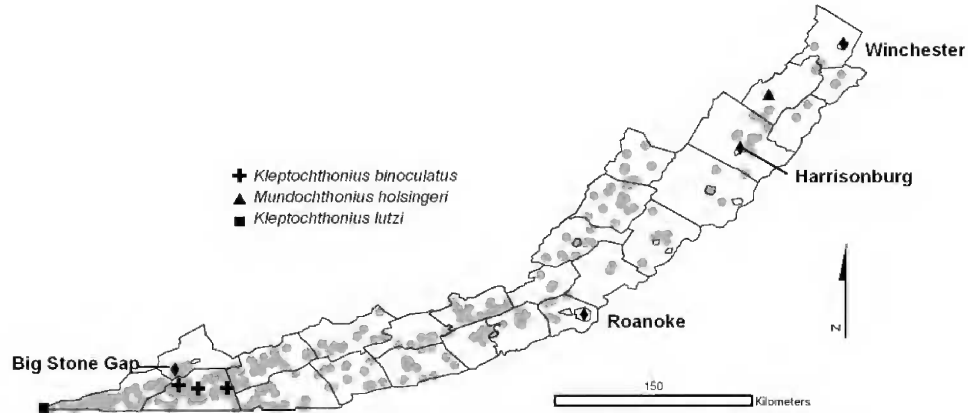


Fig. 14. Distribution of *Kleptochthonius binocularis*, *K. lutzi*, and *Mundochthonius holsingeri* in Virginia. Gray dots are all the terrestrial sampling sites.

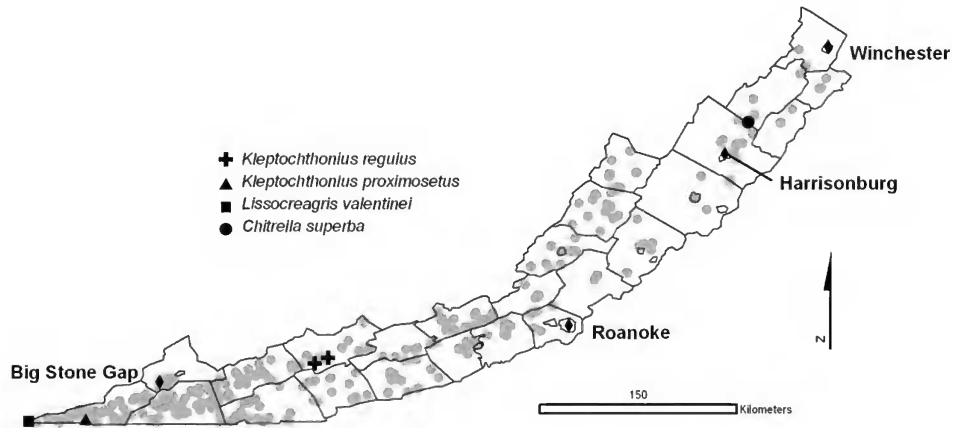


Fig. 15. Distribution of *Chitrella superba*, *Kleptochthonius proximosetus*, *K. regulus*, and *Lissocreagris valentinei* in Virginia. Gray dots are all the terrestrial sampling sites.

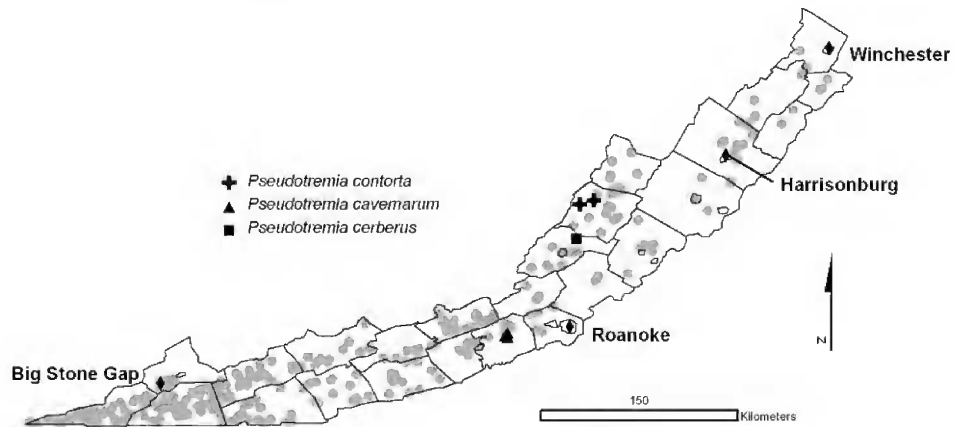


Fig. 16. Distribution of *Pseudotremia cavernarum*, *P. cerberus*, and *P. contorta* in Virginia. Gray dots are all the terrestrial sampling sites.

Class Diplopoda

Order Chordeumatida

Family Cleidogonidae

A total of 19 trogllobiotic *Pseudotremia* millipeds have been found in Virginia caves, 16 of them endemic to the state.

Pseudotremia cavernarum Cope 1869

Type Locality: Erhart Cave, Montgomery County

Other Virginia Records (Fig. 16): **Montgomery Co.**: Aunt Nellies Hole, Daves Cave, Heartbeat Cave, Unnamed Cave A.

Remarks: Listed as State Endangered in Virginia, the type locality was destroyed by quarrying. Its range is limited to approximately 40 km² in a developing suburban setting.

Pseudotremia cerberus Shear 2011

Type Locality: Wares Cave, Alleghany County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 16).

Pseudotremia contorta Shear 2011

Type Locality: Mountain Grove Saltpetre Cave, Bath County, Virginia

Other Virginia Records (Fig. 16): **Bath Co.**: Little Mountain Cave.

Remarks: Considered an epigean or somewhat troglophilic species by Shear (2011), it is currently known only from caves.

Pseudotremia culveri Shear 2011

Type Locality: Fisher Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 17).

Remarks: Occurs in the middle of the range of the more widespread *P. nodosa*.

Pseudotremia deprehendor Shear 1972

Type Locality: Feathers Cave, Anderson County, Tennessee

Virginia Record (Fig. 17): **Wise Co.**: Hairy Hole.

Remarks: Known from a few caves in eastern Tennessee.

Pseudotremia fergusonii Shear 2011

Type Locality: Stones No. 1 Cave, Smyth County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 17).

Pseudotremia hubbardi Shear 2011

Type Locality: Crackers Neck Saltpetre Cave, Wise County, Virginia

Other Virginia Records (Fig. 18): **Wise Co.**: Kelly Cave, Little Kennedy Cave, Omega Cave System, Parsons Cave, Ridge Cave, Wildcat Saltpetre Cave.

Remarks: Known only from caves near the eastern end of the Powell Valley.

Pseudotremia inexpectata Shear 2011

Type Locality: Davault Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 18).

Remarks: Occurs in the midst of the range of the more widespread *P. nodosa*.

Pseudotremia jaculohamatum Shear 2011

Type Locality: Walker Mountain Saltpetre Cave, Washington County, Virginia

Other Virginia Records (Fig. 17): none confirmed.

Remarks: Specimens from three other Washington County caves (Clarke Cave, Millard Cave, and Three Chambers Cave) are likely *P. jaculohamatum*, but confirmation is not possible due to curatorial problems (Shear, 2011).

Pseudotremia johnholsingeri Shear 2011

Type Locality: Carter Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 19).

Pseudotremia loomisi Shear 2011

Type Locality: Clarks Cave, Bath County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 18).

Remarks: According to Shear (2011), this species appears to be a troglophile rather than a true trogllobiont, but it is known only from a cave so we have included it.

Pseudotremia nodosa Loomis 1939

Type Locality: English Cave, Claiborne County, Tennessee

Virginia Records (Fig. 20): **Lee Co.**: Cavin Cave, Cedar Hill Cave, Cope Cave, Crouse Cave, Gallohan No. 1 Cave, Gallohan No. 2 Cave, Gibson-Frazier Cave, Gilley Cave, Indian Burial Cave, Jones Saltpetre Cave, Knapper Cave, Litton No. 1 Cave, Lucy Beatty Cave, Longs Cave, Molly Waggle Cave, Smith Cave, Spangler Cave, Surgener Cave, Sweet Potato Cave, Thompson Cedar Cave, Unthanks Cave, Young-Fugate Cave.

Remarks: This species is widespread in eastern Tennessee and Lee County, Virginia.

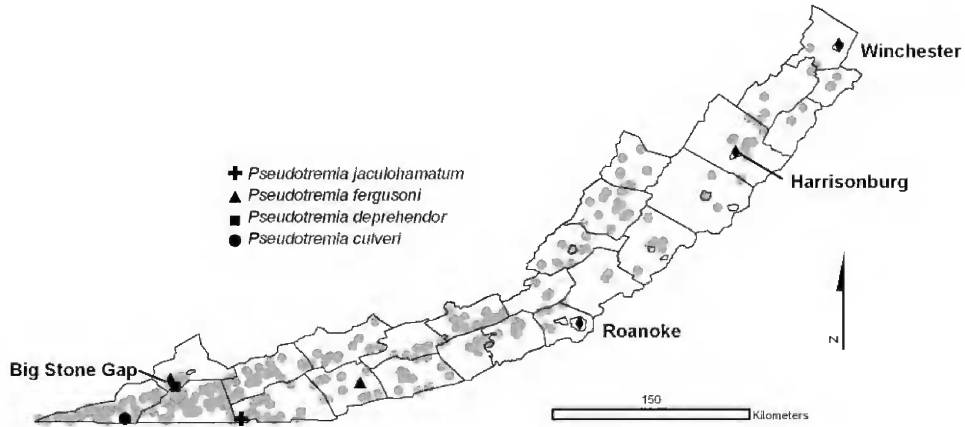


Fig. 17. Distribution of *Pseudotremia culveri*, *P. deprehendor*, *P. fergusoni*, and *P. jaculohamatum* in Virginia. Gray dots are all the terrestrial sampling sites.

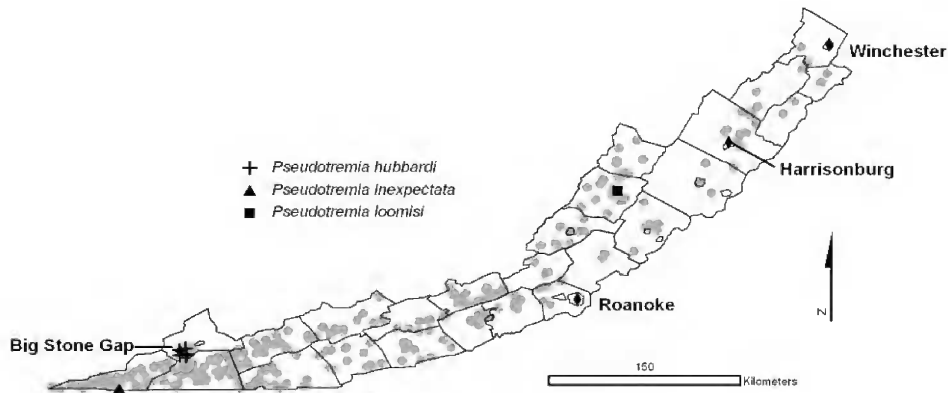


Fig. 18. Distribution of *Pseudotremia hubbardi*, *P. inexpectata*, and *P. loomisi* in Virginia. Gray dots are all the terrestrial sampling sites.

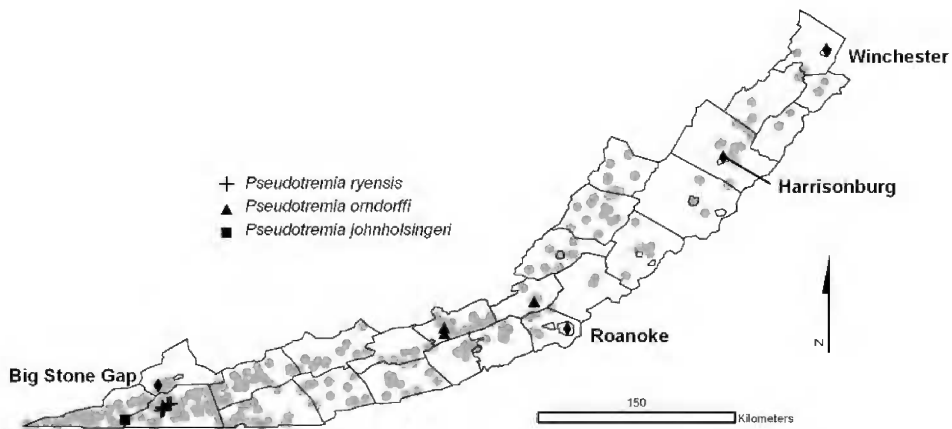


Fig. 19. Distribution of *Pseudotremia johnholsingeri*, *P. orndorffi*, and *P. ryensis* in Virginia. Gray dots are all the terrestrial sampling sites.

Pseudotremia orndorffi Shear 2011

Type Locality: Sugar Run Cave System, Giles County, Virginia

Other Virginia Records (Fig. 19): **Craig Co.**: Rufe Caldwell Cave; **Giles Co.**: Starnes Cave.

Pseudotremia peponocranium Shear 2011

Type Locality: Giant Caverns, Giles County, Virginia

Other Virginia Record (Fig. 20): **Giles Co.**: Scooters Boneyard Cave.

Pseudotremia piscator Shear 2011

Type Locality: Fisher Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 20).

Remarks: Relative to other cave-inhabiting *Pseudotremia*, this species has large eyes (21 contiguous ocelli; Shear, 2011). Perhaps, it will prove to be a troglophile.

Pseudotremia ryensis Shear 2011

Type Locality: Franklin Cave, Scott County, Virginia

Other Virginia Records (Fig. 19): **Scott Co.**: Flannery Cave, McDavids Cave, Riggs Chapel Cave, Thatcher Swallet Cave.

Remarks: The known distribution is limited to the Rye Cove area of Scott County.

Pseudotremia salifodina Shear 2011

Type Locality: Jones Saltpetre Cave, Lee County, Virginia

Other Records: Known only from the type locality (Fig. 21).

Remarks: This species shows little if any modification for subterranean life (Shear, 2011), but it is known only from a cave.

Pseudotremia tuberculata Loomis 1939

Type Locality: Cassell Farm Cave No. 2, Tazewell County, Virginia

Other Virginia Records (Fig. 21): **Tazewell Co.**: Bowens Cave, Chimney Rock Cave, Fallen Rock Cave, Lawson Cave, Stonley Cave.

Remarks: Known only from caves, but it retains eyes and pigment.

Pseudotremia valga Loomis 1943

Type Locality: Cudjo's Cavern (part of the Gap Cave System), Lee County, Virginia

Other Virginia Record (Fig. 21): **Lee Co.**: Young-Fugate Cave.

Remarks: Also known from Station Creek Cave in bordering Claiborne County, Tennessee.

Family Trichopetalidae

Zygonopus packardi Causey 1960

Type Locality: Pattons Cave, Monroe County, West Virginia

Virginia Records (Fig. 22): **Augusta Co.**: Blue Hole Cave; **Bland Co.**: Coon Cave, Hamilton Cave, Newberry-Bane Cave, Repass Saltpetre Cave; **Botetourt Co.**: Peerys Saltpetre Cave; **Craig Co.**: Loneys Cave, Rufe Caldwell Cave; **Giles Co.**: Canoe Cave, Clover Hollow Cave, Doe Mountain Cave, Echols Cave, Giant Caverns, New River Cave, Salamander Cave, Starnes Cave, Straleys No. 1 Cave, Tawneys Cave; **Montgomery Co.**: Old Mill Cave, Slussers Chapel Cave; **Page Co.**: Luray Caverns; **Pulaski Co.**: Colliers Cave, Fifty-foot Hell Cave, James Cave, Sam Bells Cave; **Roanoke Co.**: Dixie Caverns; **Wythe Co.**: Early Cave, Gardners Cave, Sam Six Cave.

Remarks: This is the most widespread of the *Zygonopus* species. It occurs syntopically with *Z. whitei* in Luray Caverns. The genus was revised by Shear (2010).

Zygonopus weyeriensis Causey 1960

Type Locality: Grand Caverns, Augusta County, Virginia

Other Virginia Records (Fig. 22): **Augusta Co.**: Madison Saltpetre Cave; **Bath Co.**: Boundless Cave, Breathing Cave, Butler-Sinking Creek Cave, Porters Cave, Russells Reserve Cave, Starr Chapel Saltpetre Cave; **Rockbridge Co.**: Billy Williams Cave, Grahams Cave.

Remarks: The entrance to Billy Williams Cave was covered during construction of Interstate 81.

Zygonopus whitei Causey 1960

Type Locality: Glade Cave, Augusta County Virginia

Other Virginia Records (Fig. 22): **Page Co.**: Luray Caverns, Ruffner No. 1 Cave; **Rockingham Co.**: 3-D Maze Cave, Bakers Cave, Cedar Hill Cave, Endless Caverns, Melrose Caverns, New Market Cave, Orebaugh Cave, Ponderosa Fissure, Stephens Cave; **Shenandoah Co.**: Maddens Cave, Shenandoah Caverns, Shenandoah Wild Cave.

Family Zosteractinidae

Ameractis satis Causey 1959

Type Locality: Indian Cave, White County, Tennessee

Virginia Records (Fig. 23): **Russell Co.**: Ferguson Hollow Cave; **Washington Co.**: Millard Cave.

Remarks: This species occurs in Alabama, Georgia, North Carolina, Tennessee, and Virginia and is the most widely distributed troglomorphic milliped in North America (Shear & Hubbard, 1998).

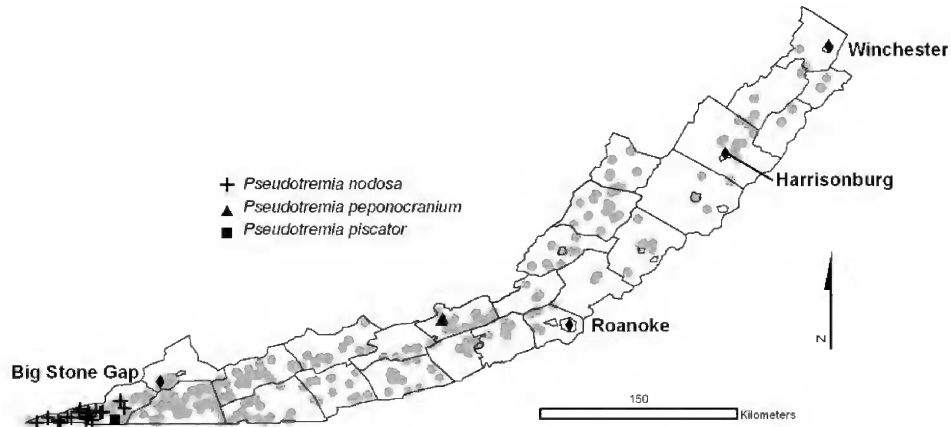


Fig. 20. Distribution of *Pseudotremia nodosa*, *P. peponocranium*, and *P. piscator* in Virginia. Gray dots are all the terrestrial sampling sites.

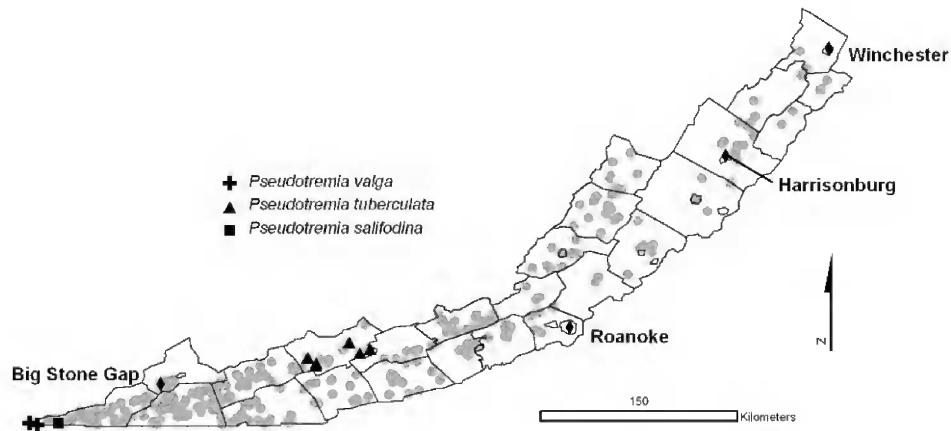


Fig. 21. Distribution of *Pseudotremia salifodina*, *P. tuberculata*, and *P. valga* in Virginia. Gray dots are all the terrestrial sampling sites.

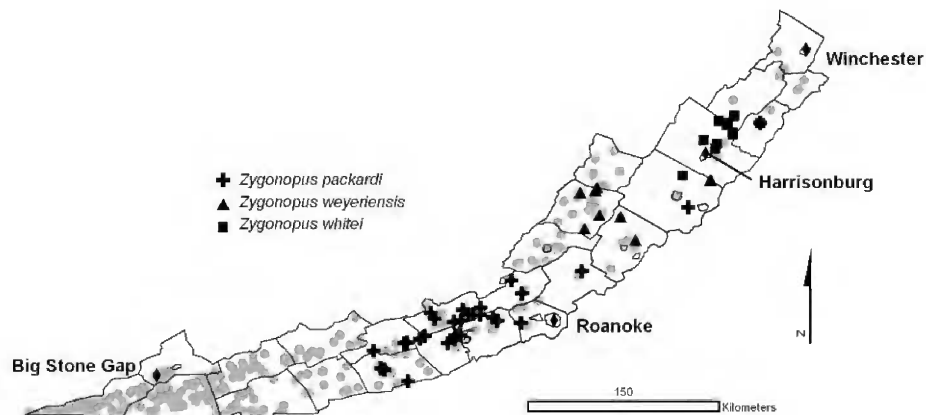


Fig. 22. Distribution of *Zygonopus packardii*, *Z. weyerienseis*, and *Z. whitei* in Virginia. Gray dots are all the terrestrial sampling sites.

Class Chilopoda**Order Lithobiomorpha****Family Lithobiidae**

Nampabius turbator Crabill 1952

Type Locality: Lowmoor Cave, Alleghany County, Virginia

Other Virginia Record (Fig. 24): **Alleghany Co.**: Island Ford Cave.

Class Hexapoda**Order Collembola****Family Entomobryidae**

Pseudosinella bona Christiansen & Bellinger 1996a

Type Locality: Goodwins Cave, Roanoke County, Virginia

Other Virginia Records (Fig. 25): **Washington Co.**: Lowes Cave; **Wythe Co.**: Chockedfullofit Cave, Williams Cave.

Pseudosinella erehwon Christiansen & Bellinger 1996a

Type Locality: Canyon to Nowhere Cave, Scott County, Virginia

Other Virginia Records (Fig. 26): **Lee Co.**: Coffin Cave; **Russell Co.**: Stewart Monks Cave; **Washington Co.**: Clarke Cave; **Wythe Co.**: Connor Valley Cave.

Pseudosinella extra Christiansen & Bellinger 1996a

Type Locality: Jack Cave, Scott County, Virginia

Other Virginia Records (Fig. 25): **Scott Co.**: Basil Duncan Cave, Lane Caves; **Wythe Co.**: Brown Cave.

Pseudosinella flatua Christiansen & Bellinger 1996a

Type Locality: Blowing Springs Cave, Swain County, North Carolina

Virginia Records (Fig. 25): **Russell Co.**: Broken Formation Cave; **Washington Co.**: Leonard Cave, Walker Mountain Saltpetre Cave.

Pseudosinella gisini virginia Christiansen & Bellinger 1996a

Type Locality: Spangler Cave, Lee County, Virginia

Other Virginia Records (Fig. 25): **Lee Co.**: Indian Burial Cave; **Russell Co.**: Daugherty Cave.

Remarks: One of three subspecies of *Pseudosinella gisini*, with *P. g. gisini* in the Greenbrier Valley of West Virginia and *P. g. carolina* from western North Carolina.

Pseudosinella granda Christiansen & Bellinger 1996a

Type Locality: Grand Caverns, Augusta County, Virginia

Other Virginia Records (Fig. 27): **Scott Co.**: Darty Cave, John W. Fugate Cave; **Washington Co.**: Whispering Breeze Cave; **Wise Co.**: Burtons Cave, Huff caves; **Wythe Co.**: Lone Ash No. 2 Cave.

Pseudosinella hirsuta Delamare Deboutteville 1949

Type Locality: Tennessee Caverns (Crystal Caves), Hamilton County, Tennessee

Virginia Records (Fig. 27): **Lee Co.**: Cliff Cave, Cudjo's Cavern (part of the Gap Cave System), Skylight Cave, Young-Fugate Cave.

Remarks: A widely distributed troglomorphic springtail in the central and southeastern U.S.

Pseudosinella ops Christiansen & Bellinger 1998

Type Locality: Herrons Echo Hall Cave, Scott County, Virginia

Other Virginia Records (Fig. 26): **Alleghany Co.**: Island Ford Cave; **Montgomery Co.**: Adams Cave; **Russell Co.**: Buffalo Hollow Hill Cave; **Washington Co.**: Leonard and Thomas No. 1 Cave.

Pseudosinella orba Christiansen 1960a

Type Locality: Morrill Cave, Sullivan County, Tennessee

Virginia Records (Fig. 28): **Bath Co.**: Starr Chapel Saltpetre Cave; **Bland Co.**: Hamilton Cave; **Botetourt Co.**: Catawba Murder Hole; **Craig Co.**: Rufe Caldwell Cave; **Giles Co.**: Starnes Cave, Sugar Run Cave System; **Lee Co.**: Cavin Cave, Gallohan No. 1 Cave, Long Cave, Smith Cave, Sweet Potato Cave; **Pulaski Co.**: Colliers Cave, Sam Bells Cave; **Roanoke Co.**: Smiths No. 1 Cave; **Russell Co.**: Austins Hilltop Cave, Concrete Tank Cave, Mountain View Cave, Porgie Bundys Cave, Stewart Monks Cave; **Scott Co.**: Blair-Collins Cave, Little Duck Cave, Sikes Cave; **Smyth Co.**: Buchanan Saltpetre Cave, Dead Air Cave, Interstate-81 Cave, Little Saltpetre Cave, Tilson Saltpetre Cave; **Tazewell Co.**: Fallen Rock Cave, Gully Cave, Higginbotham No. 1 Cave; **Washington Co.**: Fraleys Cave; **Wise Co.**: Wildcat Saltpetre Cave; **Wythe Co.**: Brown Cave, Collins Cove Cave, Macs Cave.

Remarks: Also known from caves in North Carolina, Tennessee, and West Virginia.

Pseudosinella testa Christiansen & Bellinger 1980

Type Locality: Neely Farm Cave, Mercer County, West Virginia

Virginia Record (Fig. 27): **Scott Co.**: Canyon to Nowhere Cave.

Remarks: Also known from caves in Arkansas.

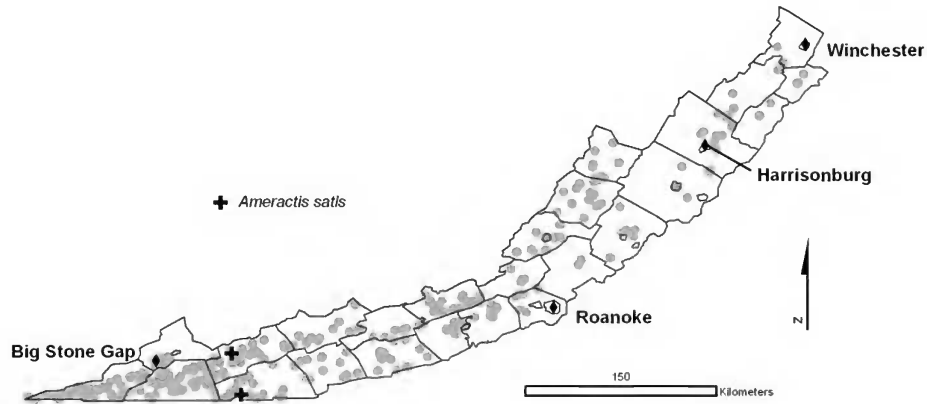


Fig. 23. Distribution of *Ameractis satls* in Virginia. Gray dots are all the terrestrial sampling sites.

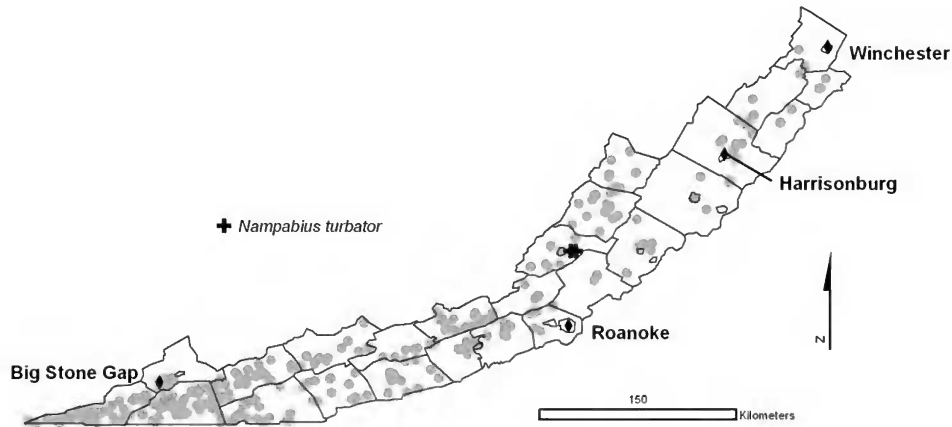


Fig. 24. Distribution of *Nampabius turbator* in Virginia. Gray dots are all the terrestrial sampling sites.

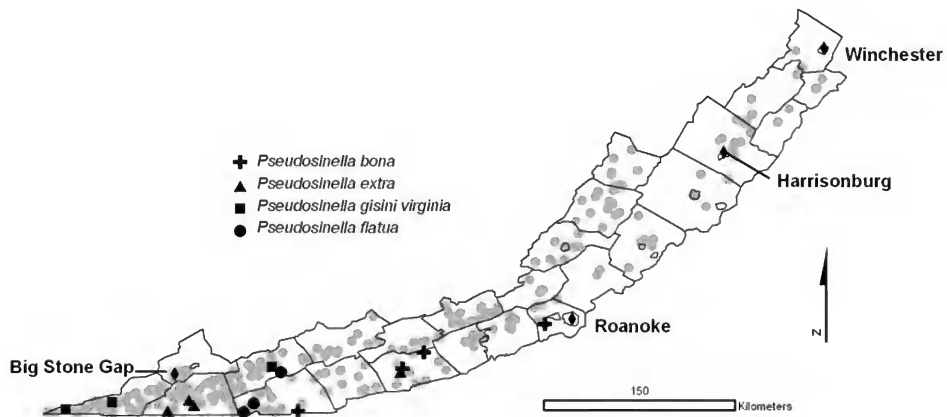


Fig. 25. Distribution of *Pseudosinella bona*, *P. extra*, *P. flatua*, and *P. gisini virginia* in Virginia. Gray dots are all the terrestrial sampling sites.

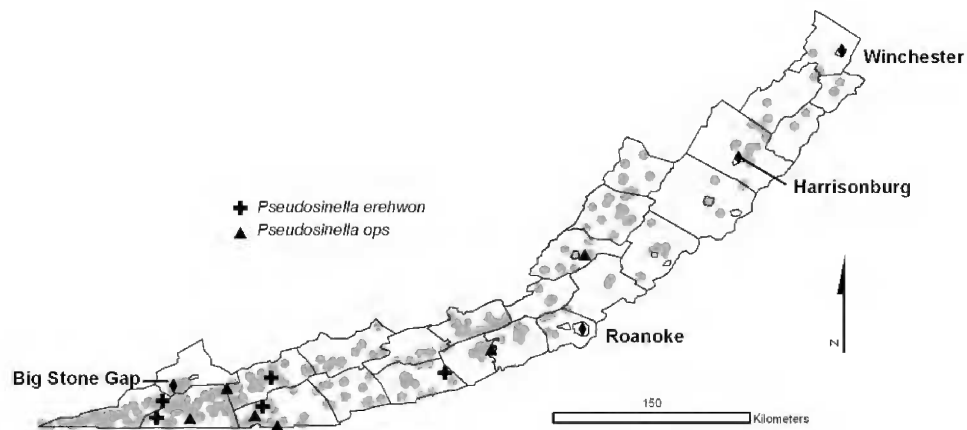


Fig. 26. Distribution of *Pseudosinella erehwon* and *P. ops* in Virginia. Gray dots are all the terrestrial sampling sites.

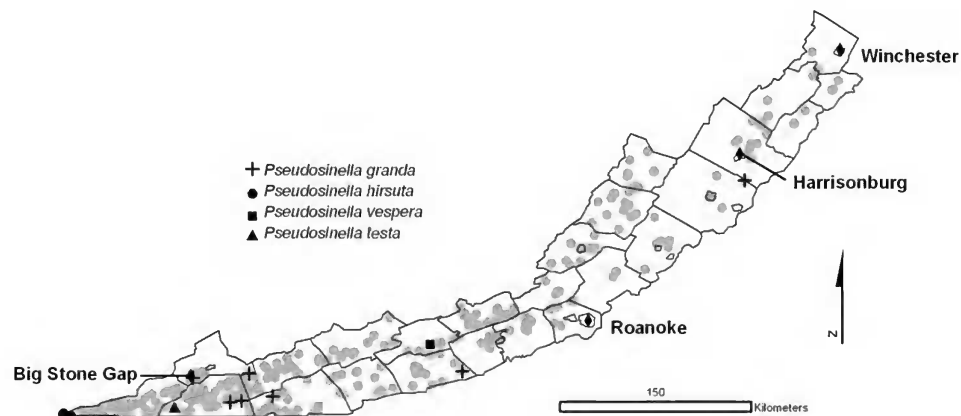


Fig. 27. Distribution of *Pseudosinella granda*, *P. hirsuta*, *P. testa*, and *P. vespera* in Virginia. Gray dots are all the terrestrial sampling sites.

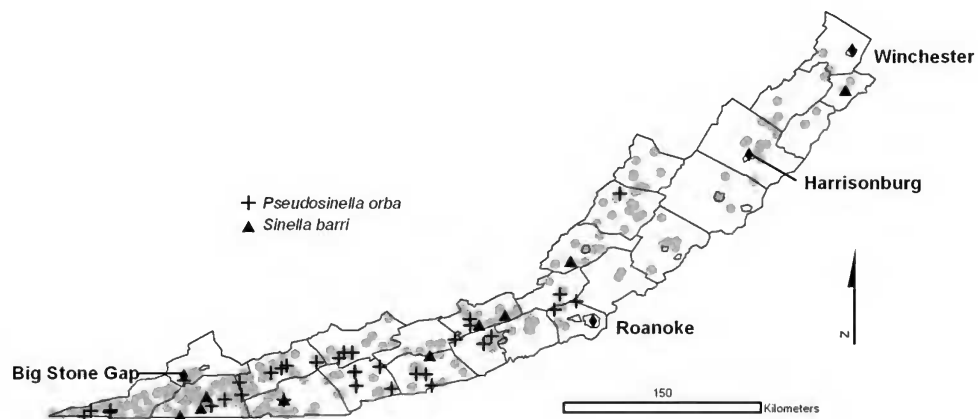


Fig. 28. Distribution of *Pseudosinella orba* and *Sinella barri* in Virginia. Gray dots are all the terrestrial sampling sites.

Pseudosinella vespera Christiansen & Bellinger 1996a
Type Locality: Bat Cave, Rutherford County, North Carolina

Virginia Record (Fig. 27): **Bland Co.**: Cedar Cliff Saltpetre Cave.

Remarks: Known from one other North Carolina cave.

Sinella barri Christiansen 1960b

Type Locality: Inman Cave, Perry County, Tennessee
Virginia Records (Fig. 28): **Alleghany Co.**: Arritt Mill Tunnel Cave; **Giles Co.**: Echols Cave, Parsells Cave; **Scott Co.**: Herrons Echo Hall Cave, McCulley Cave, Wininger Cave; **Warren Co.**: Bee Tree Cave; **Washington Co.**: Fraleys Cave, Vickers Cave; **Wythe Co.**: Picketts Cave.

Remarks: Widespread through Eastern and Midwestern states, it was originally listed by Holsinger & Culver (1988) as a troglophile, but because more than 90 percent of its localities are in caves, we list it here as a troglobiont.

Sinella hoffmani Wray 1952

Type Locality: Lowmoor Cave, Alleghany County, Virginia

Other Virginia Records (Fig. 29): **Alleghany Co.**: Blowhole Cave, Blue Spring Cave, Canterbury Cave, Island Ford Cave, Matthews No. 2 Cave, Rumbolds Cave, Walking Cave, Wares Cave; **Bath Co.**: Blowing Cave, Boundless Cave, Breathing Cave, Butler-Sinking Creek Cave, Cave Run Pit, Bicentennial Cave, Clarks Cave, Crossroads Cave, Dunns Cave, Little Mountain Cave, Little Starr Chapel Cave, Mays Mountain Saltpetre Cave, Porters Cave, Serpent Cave, Starr Chapel Saltpetre Cave, Witheros Cave; **Botetourt Co.**: Peerys Saltpetre Cave; **Highland Co.**: Cabin Cave, Helictite Cave, Hiner Cave, Secret Anthodite Cave, Sugar Maple Cave, Vandevander Cave, Water Sinks Cave; **Lee Co.**: Glen Olingers Cave; **Roanoke Co.**: Goodwins Cave; **Rockbridge Co.**: Buck Hill Cave, Doll House Cave, Turkey Hill Cave; **Rockingham Co.**: Devil's Hole, Raindrops a Dripping Cave; **Russell Co.**: Cascade Pit; **Scott Co.**: M.J. Mann Cave, Cave Hollow Cave; **Tazewell Co.**: Stonley Cave; **Washington Co.**: Three Chambers Cave; **Wise Co.**: Bloomer Cave; **Wythe Co.**: Connor Valley Cave.

Remarks: Widespread in the central and southern Appalachians.

Family Hypogastruridae

Schaefferia hubbardi Thibaud 1995

Type Locality: Hiner Cave, Highland County, Virginia
Other Virginia Records (Fig. 30): **Pulaski Co.**: Maze

Cave; **Russell Co.**: Family Secret Cave; **Scott Co.**: Greears Sweet Potato Cave.

Schaefferia valentini Thibaud 1996

Type Localities: Grigsby and Herrons Echo Hall caves, Scott County, Virginia

Other Virginia Records (Fig. 30): **Giles Co.**: Echols Cave; **Pulaski Co.**: Colliers Cave, Maze Cave; **Russell Co.**: Amos Cave, Densmore Hill Cave, Sentinel Oak Cave, Smiths Drop Cave; **Scott Co.**: Little Duck Cave, M.J. Mann Cave, Prince Albert in a Cave, Queens Cave, Sikes Cave; **Washington Co.**: Robinson Cave; **Wythe Co.**: Blue Grotto Cave, Brown Cave, Collins Cove Cave, Early Cave, Sam Six Cave.

Family Neanuridae

Paleonura petebellingeri Palacios-Vargas & Benito 2007

Type Locality: Skyline Caverns, Warren County, Virginia

Other Records: Known only from the type locality (Fig. 31).

Speleonura kenchristianseni Palacios-Vargas & Benito 2007

Type Locality: Porters Cave, Bath County, Virginia

Other Records: Known only from the type locality (Fig. 31).

Remarks: This is the only species currently known in its genus.

Family Oncopoduridae

Oncopodura hubbardi Christiansen & Bellinger 1996a

Type Locality: Reasors Cave, Lee County, Virginia

Other Virginia Records (Fig. 32): **Lee Co.**: Burton Cave, Cattle Cave, Spangler Cave; **Scott Co.**: Carters Pit, Jesse Branch Cave.

Remarks: Known only from the Upper Tennessee River basin in southwestern Virginia.

Family Sminthuridae

Pygmarrhopalites caedus (Christiansen & Bellinger 1996b)

Type Locality: Catawba Murder Hole, Botetourt County, Virginia

Other Virginia Records (Fig. 32): **Bath Co.**: Little Starr Chapel Cave, Starr Chapel Saltpetre Cave.

Remarks: Relatively unmodified for subterranean life, it is known only from caves in the Alleghany Highlands of Virginia.

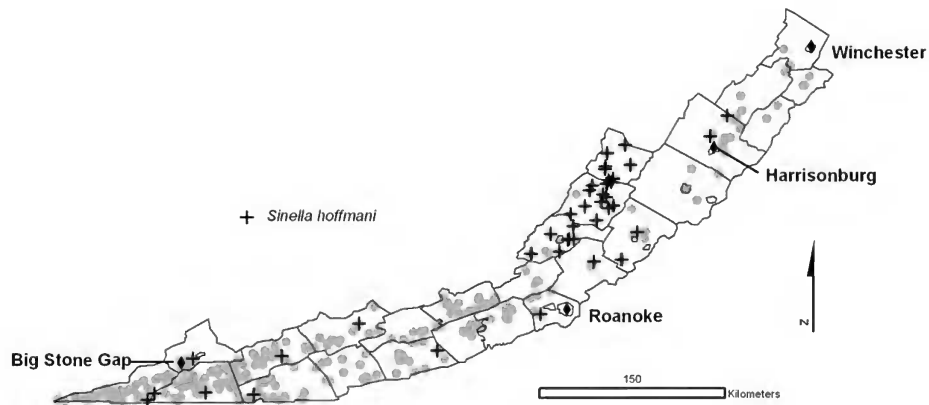


Fig. 29. Distribution of *Sinella hoffmani* in Virginia. Gray dots are all the terrestrial sampling sites.

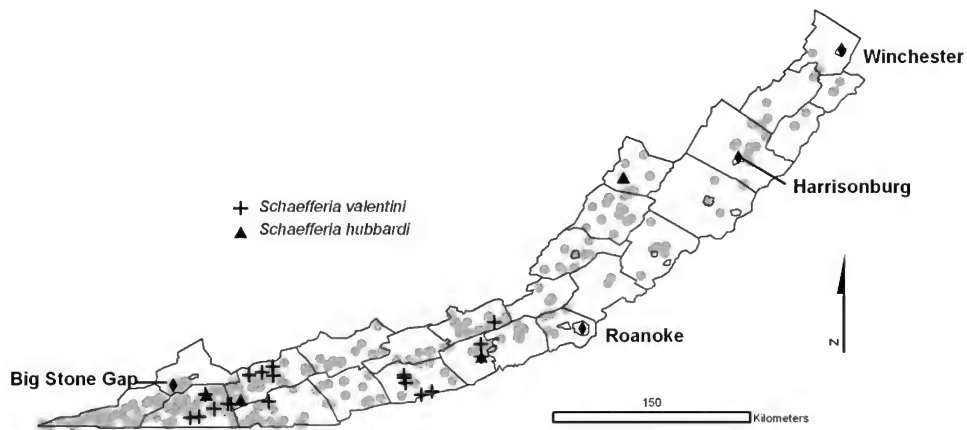


Fig. 30. Distribution of *Schaefferia hubbardi* and *S. valentini* in Virginia. Gray dots are all the terrestrial sampling sites.

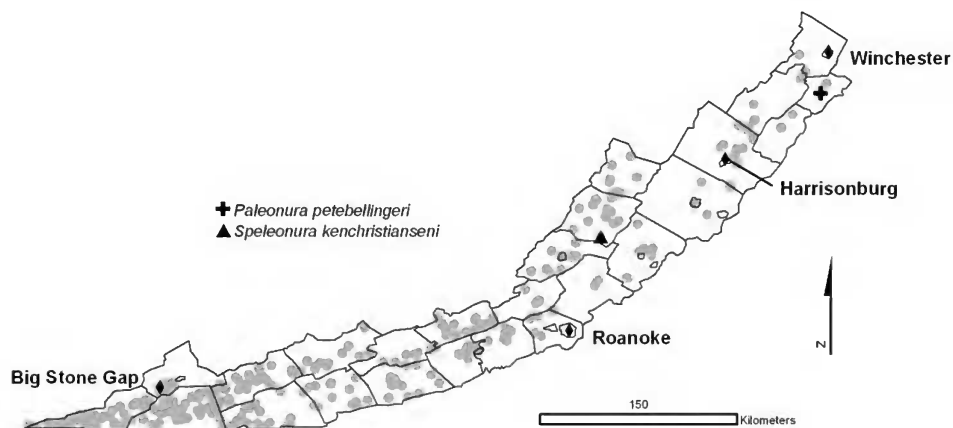


Fig. 31. Distribution of *Paleonura petebellingeri* and *Speleonura kenchristianseni* in Virginia. Gray dots are all the terrestrial sampling sites.

Pygmarrhopalites carolynae (Christiansen & Bellinger 1996b)

Type Locality: Wildcat Saltpetre Cave, Wise County, Virginia

Other Virginia Records (Fig. 33): **Alleghany Co.**: Matthews No. 2 Cave; **Augusta Co.**: Staunton Quarry Cave; **Bath Co.**: Butler-Sinking Creek Cave, Little Starr Chapel Cave, Starr Chapel Saltpetre Cave; **Botetourt Co.**: Peerys Saltpetre Cave; **Highland Co.**: Marshalls Cave, Water Sinks Cave; **Lee Co.**: Spangler Cave; **Russell Co.**: Tumbez Cave; **Shenandoah Co.**: Crystal Caverns at Hupps Hill; **Wythe Co.**: Lone Ashe No. 2 Cave.

Remarks: This species is highly variable morphologically, and is also known from caves in Indiana.

Pygmarrhopalites clarus (Christiansen 1966)

Type Locality: Rockhouse Cave, Barry County, Missouri

Virginia Records (Fig. 34): **Bath Co.**: Starr Chapel Saltpetre Cave; **Montgomery Co.**: Old Mill Cave; **Wythe Co.**: Campbell Cave, Gardners Cave, Sam Six Cave.

Remarks: A strongly troglomorphic species, widespread through Eastern and Midwestern states.

Pygmarrhopalites commorus (Christiansen & Bellinger 1996b)

Type Locality: Stay High Cave, Giles County, Virginia

Other Virginia Records (Fig. 34): **Lee Co.**: Burton Cave; **Scott Co.**: Queens Cave; **Wise Co.**: Big Kennedy Cave, Little Kennedy Cave.

Remarks: Also known from a cave in Pocahontas Co., West Virginia.

Pygmarrhopalites lacuna (Christiansen & Bellinger 1996b)

Type Locality: Paxtons Cave, Alleghany County, Virginia

Other Virginia Record (Fig. 32): **Wise Co.**: Kelly Cave.

Pygmarrhopalites marshalli (Christiansen & Bellinger 1996b)

Type Locality: Wininger Cave, Scott County, Virginia

Other Virginia Records (Fig. 33): **Giles Co.**: Echols Cave; **Highland Co.**: Helictite Cave; **Russell Co.**: Burns Cave, Concrete Tank Cave, Daugherty Cave, Dorton Springs Cave, Mountain View Cave, Phreatic to a Fault Cave, Sentinel Oak Cave, Stewart Monks Cave; **Scott Co.**: Canyon to Nowhere Cave, Dancing Rock Cave, Darty Cave, Hartsock Cave, Jack Hartsock Cave, Jessee Branch Cave, Jim Robinson Cave, Sounding Cave; **Smyth Co.**: Little Saltpetre Cave; **Tazewell Co.**:

Chimney Rock Cave; **Washington Co.**: Fraleys Cave; **Wythe Co.**: Minnie Corvins Cave.

Remarks: Also known from caves in northeastern Tennessee.

Pygmarrhopalites obtusus (Zeppelini & Christiansen 2003)

Type Locality: Bakers Cave, Rockingham County, Virginia

Other Virginia Record (Fig. 33): **Rockingham Co.**: Orebaugh Cave.

Pygmarrhopalites pavo (Christiansen & Bellinger 1996b)

Type Locality: Turkey Hill Cave, Rockbridge County, Virginia

Other Virginia Records (Fig. 35): **Rockbridge Co.**: Ringbat Pothole Cave; **Scott Co.**: Bolling Cave, Wininger Cave.

Remarks: Also known from caves in Tennessee and West Virginia.

Pygmarrhopalites sacer (Christiansen & Bellinger 1996b)

Type Locality: Little Starr Chapel Cave, Bath County, Virginia

Other Virginia Records (Fig. 34): **Bath Co.**: Butler-Sinking Creek Cave, Barberry Cave, Starr Chapel Saltpetre Cave; **Pulaski Co.**: Colliers Cave; **Tazewell Co.**: Hugh Young Cave.

Remarks: Also known from caves in Monroe County, West Virginia.

Pygmarrhopalites sextus (Zeppelini & Christiansen 2003)

Type Locality: Sam Six Cave, Wythe County, Virginia

Other Virginia Record (Fig. 35): **Wythe Co.**: Irvin Cave.

Remarks: Known only from one Virginia county.

Pygmarrhopalites silvus (Christiansen & Bellinger 1996b)

Type Locality: Woods-Terry Cave, Highland County, Virginia

Other Virginia Records (Fig. 35): **Bath Co.**: Clarks Cave; **Highland Co.**: Hiner Cave.

Order Diplura

Family Campodeidae

Litocampa cookei (Packard 1871)

Type Locality: Mammoth Cave, Edmonson County, Kentucky

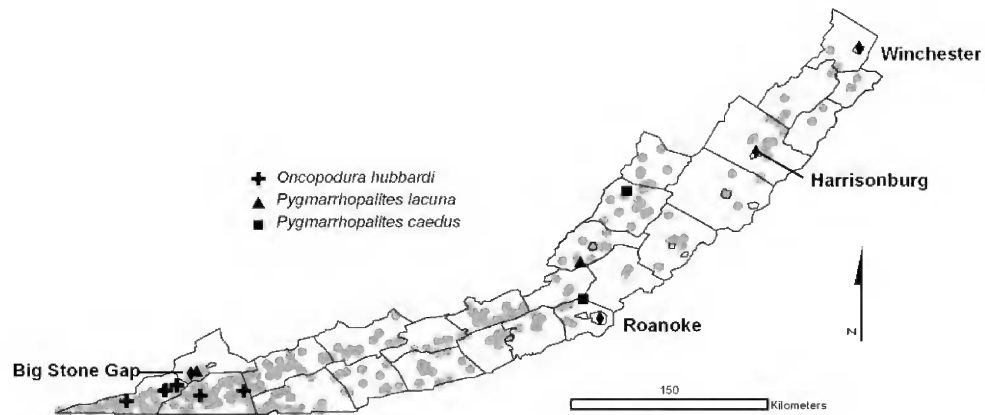


Fig. 32. Distribution of *Oncopodura hubbardi*, *Pygmarrhopalites caedus*, and *P. lacuna* in Virginia. Gray dots are all the terrestrial sampling sites.

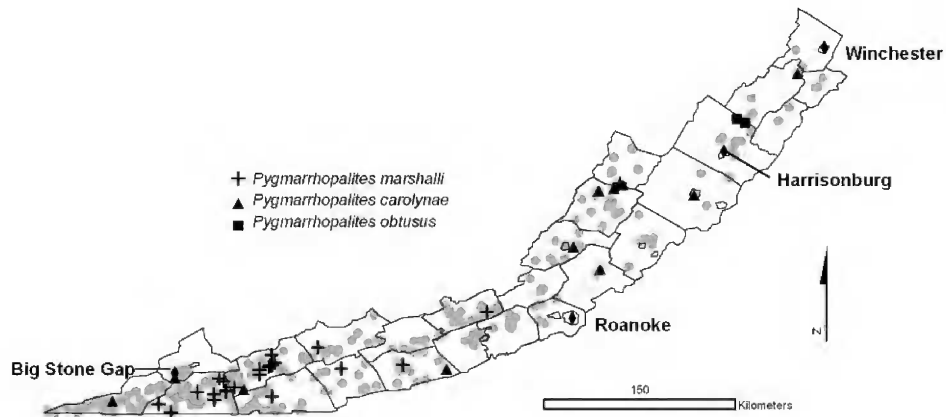


Fig. 33. Distribution of *Pygmarrhopalites carolynae*, *P. marshalli*, and *P. obtusus* in Virginia. Gray dots are all the terrestrial sampling sites.

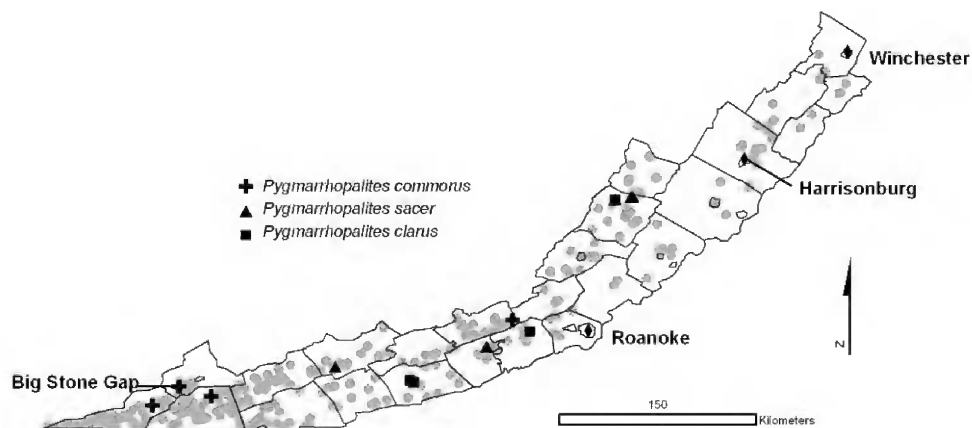


Fig. 34. Distribution of *Pygmarrhopalites clarus*, *P. commorus*, and *P. sacer* in Virginia. Gray dots are all the terrestrial sampling sites.

Virginia Records (Fig. 36): **Lee Co.**: Cave Road Cave, Gallohan No. 1 Cave, Garretts Cave, Jones Saltpetre Cave, Long Cave, Molly Wagle Cave, Mud Cave, Sweet Potato Cave, Young-Fugate Cave; **Scott Co.**: Cave Hollow Cave, Spurlock Cave; **Wise Co.**: Big Kennedy Cave, Crackers Neck Saltpetre Cave, Hairy Hole, Little Kennedy Cave, Parsons Cave, Rocky Hollow Cave.

Remarks: There are a number of undescribed species in the genus. This species is also recorded from caves in east and middle Tennessee and south-central Kentucky.

Litocampa fieldingae (Condé 1949)

Type Locality: McClungs Cave, Greenbrier County, West Virginia

Virginia Records (Fig. 36): **Highland Co.**: Aqua Cave. Remarks: Occurs in a number of caves in Monroe, Greenbrier, and Pocahontas counties, West Virginia (Fong et al., 2007).

Litocampa hoffmani Ferguson 2009

Type Locality: Speedwell Cave No. 1, Wythe County, Virginia

Other Virginia Records (Fig. 36): **Montgomery Co.**: Vicker Road Cave; **Smyth Co.**: Dead Air Cave, Interstate-81 Cave, Overbay Hill Cave, Roberts Cave, Ward Saltpetre Cave; **Washington Co.**: Brass Kettle Hole, Ira Miller Cave, Maddens Pyramid Cave; **Wythe Co.**: Groseclose No. 1 Cave.

Litocampa pucketti Condé & Bareth 1996

Type Locality: Lawson Cave, Tazewell County, Virginia

Other Virginia Records (Fig. 36): **Bland Co.**: Hamilton Cave; **Giles Co.**: Harris Cave; **Tazewell Co.**: Cassell Farm No. 2 Cave.

Class Insecta

Order Coleoptera

Family Carabidae

A total of 31 species of *Pseudanophthalmus* have been found in Virginia caves, 29 of them endemic to the state.

Pseudanophthalmus avernus (Valentine 1945)

Type Locality: Endless Caverns, Rockingham County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 37).

Remarks: This beetle is typically seen on sediment banks along the stream in the non-commercial sections of this popular commercial cave.

Pseudanophthalmus cordicollis Barr 1981

Type Locality: Little Kennedy Cave, Wise County, Virginia

Other Virginia Records (Fig. 37): **Wise Co.**: Franklins Pit, Omega Cave System, Wildcat Saltpetre Cave.

Pseudanophthalmus deceptivus Barr 1981

Type Locality: Fisher Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 37).

Pseudanophthalmus delicatus Valentine 1932

Type Locality: Gilley Cave, Lee County, Virginia

Other Virginia Records (Fig. 38): **Lee Co.**: Baileys Cave, Bowling Cave, Burial Cave, Cattle Cave, Gallohan No. 1 Cave, Garretts Cave, Gibson No. 1 Cave, Jones Saltpetre Cave, Litton No. 1 Cave, McCurry Indian Cave, Molly Wagle Cave, Poor Farm Cave, Seal Pit, Smith Cave, Spangler Cave, Unthanks Cave.

Remarks: This is one of the most widespread species of *Pseudanophthalmus* in the Commonwealth, yet it is confined to a single county.

Pseudanophthalmus egberti Barr 1965

Type Locality: Starnes Cave, Giles County, Virginia

Other Virginia Record (Fig. 37): **Giles Co.**: Giant Caverns.

Pseudanophthalmus gracilis Valentine 1931

Type Locality: Tawneys Cave, Giles County, Virginia

Other Virginia Records (Fig. 38): **Craig Co.**: Rufe Caldwell Cave; **Giles Co.**: Clover Hollow Cave, Smokehole Cave, Stay High Cave.

Pseudanophthalmus hirsutus Valentine 1931

Type Locality: Cudjo's Cavern (part of the Gap Cave System), Lee County, Virginia

Other Virginia Record (Fig. 39): **Lee Co.**: Cumberland Gap Saltpetre Cave (part of the Gap Cave System).

Remarks: Both of these caves are now part of the Cumberland Gap Cave System.

Pseudanophthalmus hoffmani Barr 1965

Type Locality: Buchanan Saltpetre Cave, Smyth County, Virginia

Other Virginia Records (Fig. 38): **Bland Co.**: Byrds Water Cave, Coon Cave, Hamilton Cave, Newberry-Bane Cave, Repass Saltpetre Cave; **Giles Co.**: Salamander Cave; **Smyth Co.**: Beaver Creek Cave,

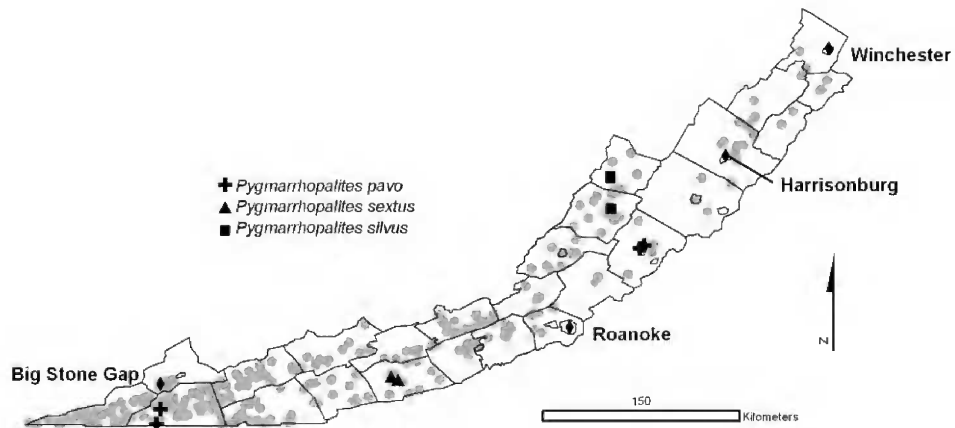


Fig. 35. Distribution of *Pygmarhopalties pavo*, *P. sextus*, and *P. silvus* in Virginia. Gray dots are all the terrestrial sampling sites.

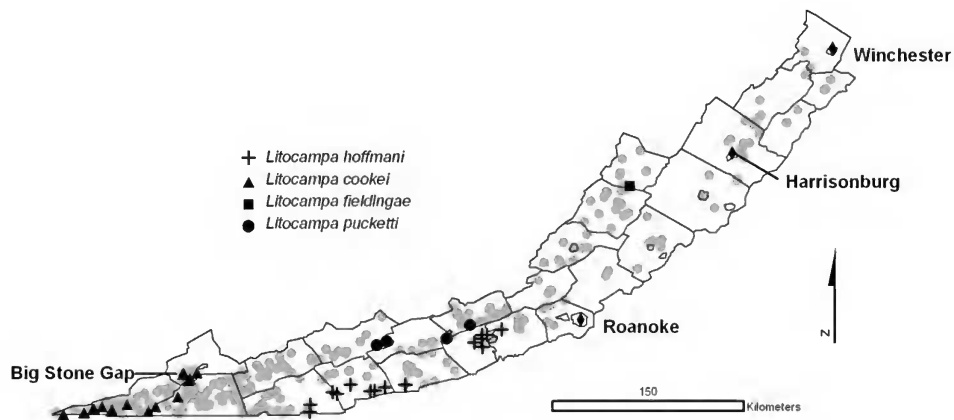


Fig. 36. Distribution of *Litocampa cookei*, *L. fieldingae*, *L. hoffmani*, and *L. pucketti* in Virginia. Gray dots are all the terrestrial sampling sites.

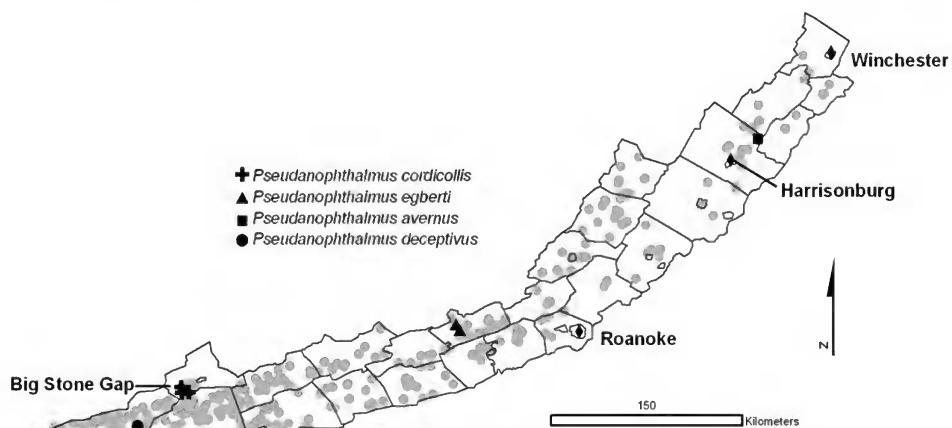


Fig. 37. Distribution of *Pseudanophthalmus avernus*, *P. cordicollis*, *P. deceptivus*, and *P. egberti* in Virginia. Gray dots are all the terrestrial sampling sites.

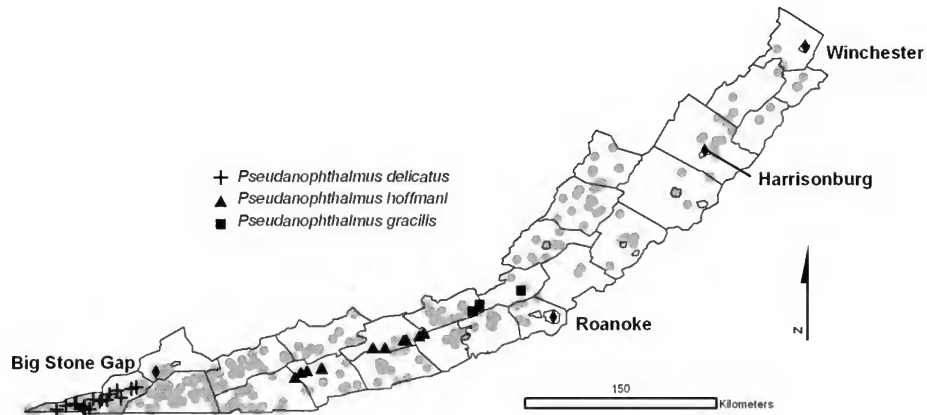


Fig. 38. Distribution of *Pseudanophthalmus delicatus*, *P. gracilis*, and *P. hoffmani* in Virginia. Gray dots are all the terrestrial sampling sites.

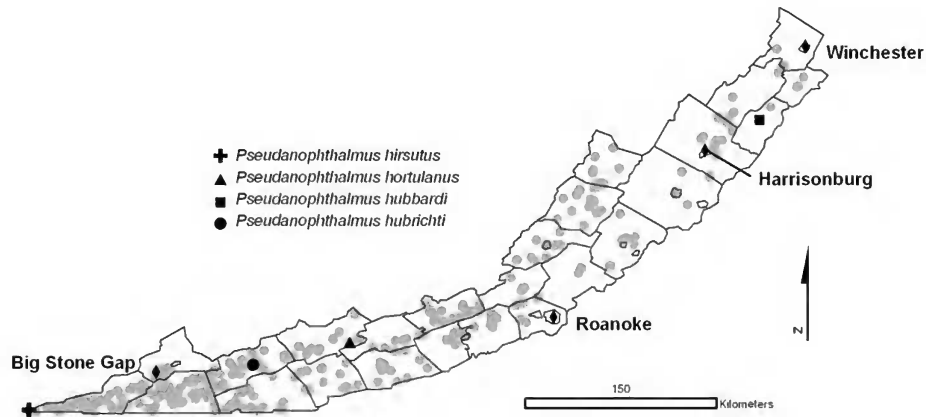


Fig. 39. Distribution of *Pseudanophthalmus hirsutus*, *P. hortulanus*, *P. hubbardi*, and *P. hubrichti* in Virginia. Gray dots are all the terrestrial sampling sites.

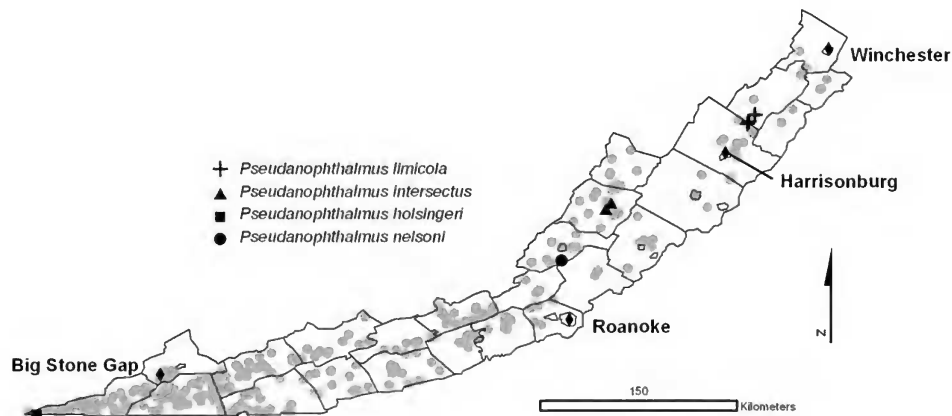


Fig. 40. Distribution of *Pseudanophthalmus holsingeri*, *P. intersectus*, *P. limicola*, and *P. nelsoni* in Virginia. Gray dots are all the terrestrial sampling sites.

Marble Cave, Walkers Cave; **Washington Co.:** Quarry No. 1 Cave.

Remarks: Range extensions into both Giles and Washington counties as well as the new Byrds Water Cave record in Bland County supplement records in Holsinger & Culver (1988) and Barr (2004).

Pseudanophthalmus holsingeri Barr 1965

Type Locality: Young-Fugate Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 40).

Remarks: This species is listed as State Endangered.

Pseudanophthalmus hortulanus Barr 1965

Type Locality: Cassell Farm No. 2 Cave, Tazewell County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 39).

Pseudanophthalmus hubbardi (Barber 1928)

Type Locality: Luray Caverns, Page County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 39).

Remarks: Barr (2004) erroneously reported that this species had "not been retaken for several decades, perhaps because of commercialization of the cave." In fact, Hubbard collected both male and female specimens, with and without bait, near Broadus Lake in Luray Caverns in February 1996.

Pseudanophthalmus hubrichti Valentine 1948

Type Locality: Daugherty Cave, Russell County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 39).

Pseudanophthalmus intersectus Barr 1965

Type Locality: Crossroads Cave, Bath County, Virginia

Other Virginia Record (Fig. 40): **Bath Co.:** Williams Cave.

Pseudanophthalmus limicola Jeannel 1931

Type Locality: Maddens Cave, Shenandoah County, Virginia

Other Virginia Records (Fig. 40): **Rockingham Co.:** Bakers Cave; **Shenandoah Co.:** Shenandoah Caverns, Shenandoah Wild Cave.

Pseudanophthalmus longiceps Barr 1981

Type Locality: Fisher Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 41).

Pseudanophthalmus nelsoni Barr 1965

Type Locality: Artritt Mill Tunnel Cave, Alleghany County, Virginia

Other Virginia Record (Fig. 40): **Alleghany Co.:** Blue Springs Cave.

Pseudanophthalmus parvicollis Jeannel 1931

Type Locality: Battlefield Crystal Cave, Shenandoah County, Virginia

Other Virginia Record (Fig. 41): **Frederick Co.:** Ogdens Cave.

Remarks: Repeated attempts by Hubbard to find this species at its type locality, even with bait, met with failure in March 1992, June 1998, November 1998, and February 1999. This commercial cave is presently known as Crystal Caverns at Hupps Hill.

Pseudanophthalmus petrunkevitchi Valentine 1945

Type Locality: Skyline Caverns, Warren County, Virginia

Other Virginia Records (Fig. 41): **Page Co.:** Woods Cave; **Warren Co.:** Allens Cave.

Pseudanophthalmus pontis Barr 1965

Type Locality: Buck Hill Cave, Rockbridge County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 41).

Remarks: Repeated attempts to find this species at its type locality, even with bait, have met with failure beginning in November 1992. Environmental changes accompanying the commercialization of this cave (Natural Bridge Caverns) are thought to have adversely affected and possibly extirpated this species.

Pseudanophthalmus potomaca Valentine 1932

Type Locality: Kenny Simmons Cave, Pendleton County, West Virginia

Virginia Records (Fig. 42): **Bath Co.:** Little Mountain Cave, Starr Chapel Saltpetre Cave; **Highland Co.:** Vandevander Cave.

Remarks: The range extension into Bath County supplements records in Holsinger & Culver (1988) and Barr (2004).

Pseudanophthalmus praetermissus Barr 1981

Type Locality: Kerns No. 1 Cave, Scott County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 42).

Pseudanophthalmus punctatus Valentine 1931

Type Locality: Tawneys Cave, Giles County, Virginia

Other Virginia Records (Fig. 42): **Giles Co.:** Clover

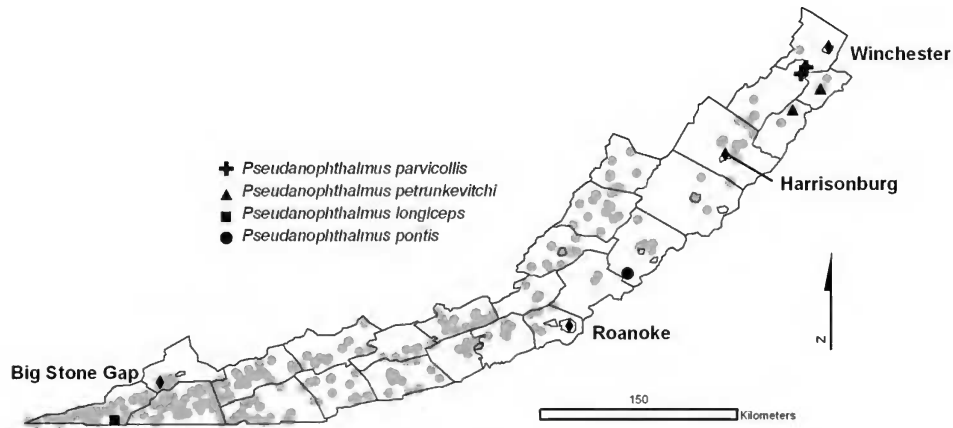


Fig. 41. Distribution of *Pseudanophthalmus longiceps*, *P. parvicollis*, *P. petrunkevitchi*, and *P. pontis* in Virginia. Gray dots are all the terrestrial sampling sites.

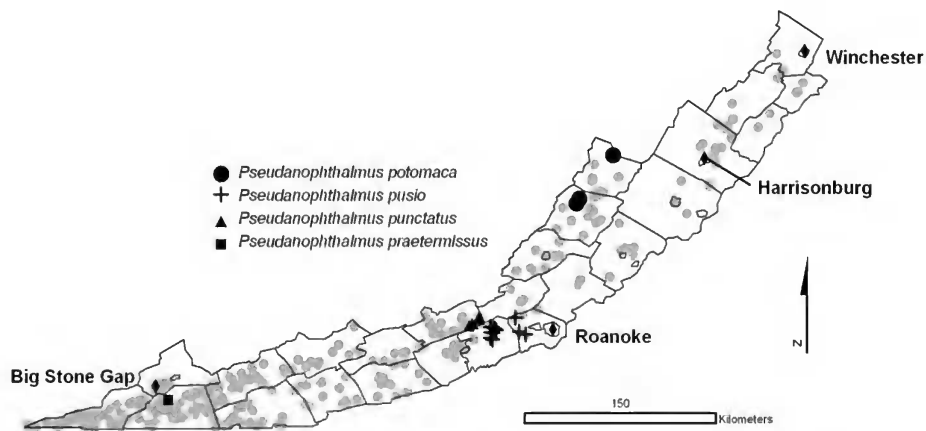


Fig. 42. Distribution of *Pseudanophthalmus potomaca*, *P. praetermissus*, *P. punctatus*, and *P. pusio* in Virginia. Gray dots are all the terrestrial sampling sites.

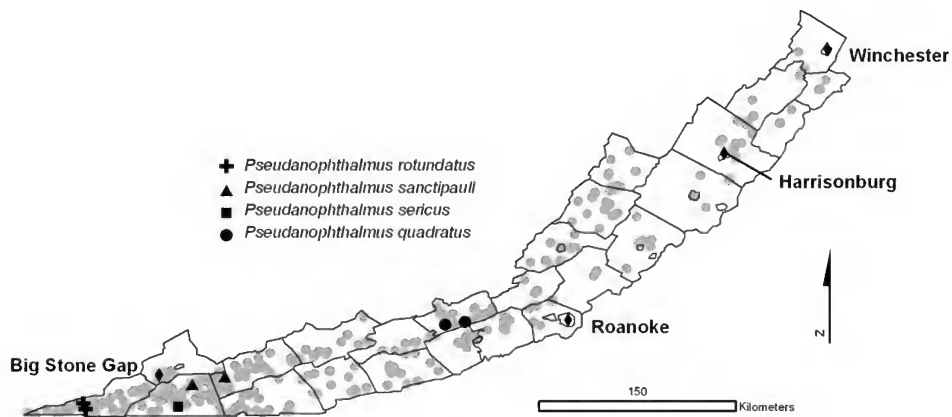


Fig. 43. Distribution of *Pseudanophthalmus quadratus*, *P. rotundatus*, *P. sanctipauli*, and *P. sericus* in Virginia. Gray dots are all the terrestrial sampling sites.

Hollow Cave, Smokehole Cave, Spruce Run Mountain Cave, Stay High Cave.

Remarks: The Stay High Cave record of this species supplements its reporting in Holsinger & Culver (1988) and Barr (2004).

Pseudanophthalmus pusio (Horn 1868)

Type Locality: Erhart Cave, Montgomery County, Virginia

Other Virginia Records (Fig. 42): **Montgomery Co.:** Agnews Cave, Aunt Nellies Hole, Fred Bulls Cave, Mill Creek Cave, Old Mill Cave, Slussers Chapel Cave, Thorn Hill Cave; **Roanoke Co.:** Goodwins Cave, New Dixie Cave, Smith No. 1 Cave.

Remarks: The type locality was destroyed by quarrying (Barr, 2004).

Pseudanophthalmus quadratus Barr 1965

Type Locality: Straleys No. 1 Cave, Giles County, Virginia

Other Virginia Record (Fig. 43): **Giles Co.:** Sugar Run Cave System.

Remarks: The Sugar Run Cave System record of this species supplements its reporting in Holsinger & Culver (1988).

Pseudanophthalmus rotundatus Valentine 1932

Type Locality: English Cave, Claiborne County, Tennessee

Virginia Records (Fig. 43): **Lee Co.:** Elys Moonshine Cave, Smith Cave, Sweet Potato Cave.

Pseudanophthalmus sanctipauli Barr 1981

Type Locality: Banners Corner Cave, Russell County, Virginia

Other Virginia Record (Fig. 43): **Scott Co.:** Greears Sweet Potato Cave.

Pseudanophthalmus seclusus Barr 1981

Type Locality: Flannery Cave, Scott County, Virginia

Other Virginia Records (Fig. 44): **Scott Co.:** Alley Cave, Cox Ram Pump Cave, Hill Cave, Kerns No. 1 Cave, McDavids Cave, Pond Cave, Queens Cave.

Pseudanophthalmus sericus Barr 1981

Type Locality: Lane Cave, Scott County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 43).

Pseudanophthalmus thomasi Barr 1981

Type Locality: Blair-Collins Cave, Scott County, Virginia

Other Virginia Record (Fig. 45): **Scott Co.:** Coley No. 2 Cave.

Remarks: This species is listed as State Endangered.

Pseudanophthalmus vicarius Barr 1965

Type Locality: Hugh Young Cave, Tazewell County, Virginia

Other Virginia Records (Fig. 44): **Tazewell Co.:** Bowens Cave, Cauliflower Cave, Fallen Rock Cave, Gully Cave, Lost Mill No. 3 Cave, Martins Cave.

Pseudanophthalmus virginicus (Barr 1960)

Type Locality: Hugh Young Cave, Tazewell County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 45).

Remarks: This species was originally the type species of the genus *Aphanotrechus* but is now assigned to *Pseudanophthalmus*.

Family Pselaphidae

Arianops jeanneli Park 1956

Type Locality: Gilley Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 46).

Order Diptera

Family Sphaeroceridae

Spelobia tenebrarum (Aldrich 1897)

Type Locality: Wyandotte Cave, Crawford County, Indiana

Virginia Records (Fig. 47): **Lee Co.:** Molly Wagle Cave, Sweet Potato Cave.

Remarks: This fly, often associated with dung, is widespread in caves throughout the eastern United States. It has not been routinely collected, and is undoubtedly much more common and widespread in Virginia than the two records indicate.

Class Malacostraca

Order Amphipoda

Family Crangonyctidae

Bactrurus angulus Koenemann & Holsinger 2001

Type Locality: Saur Kraut Cave, Claiborne County, Tennessee

Virginia Record (Fig. 48): **Lee Co.:** Cumberland Gap Saltpetre Cave (part of the Gap Cave System)

Remarks: This large, rare species is also recorded from Kings Saltpetre Cave, Claiborne Co., Tennessee.

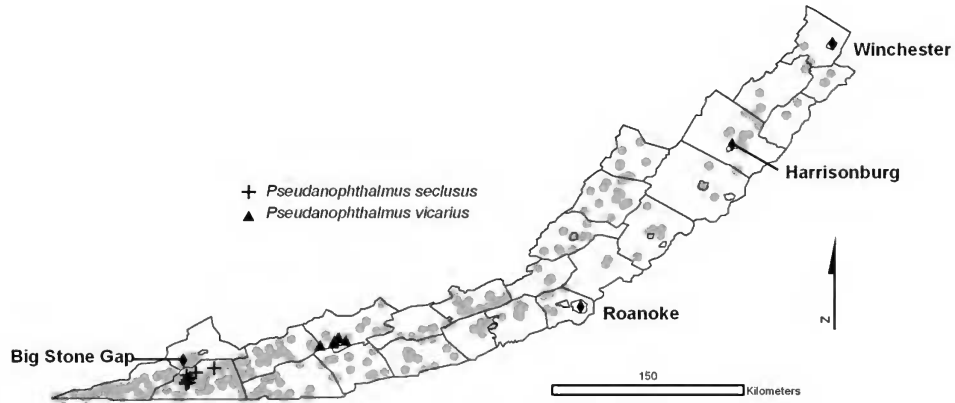


Fig. 44. Distribution of *Pseudanophthalmus seclusus* and *P. vicarius* in Virginia. Gray dots are all the terrestrial sampling sites.

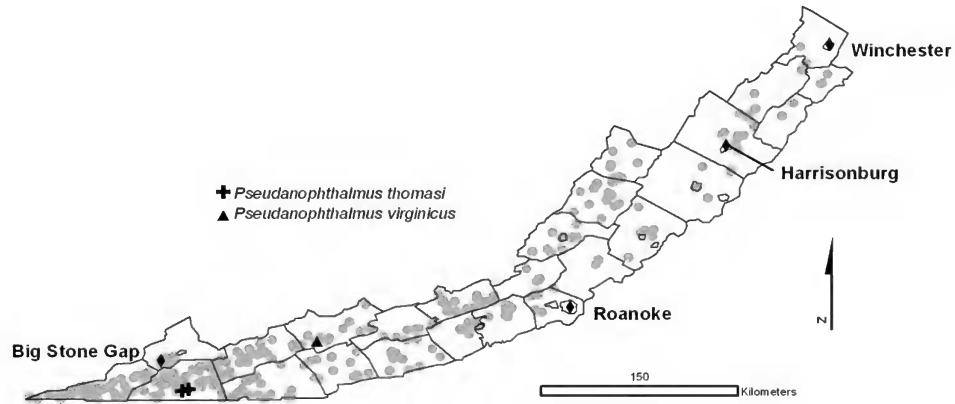


Fig. 45. Distribution of *Pseudanophthalmus thomasi* and *P. virginicus* in Virginia. Gray dots are all the terrestrial sampling sites.

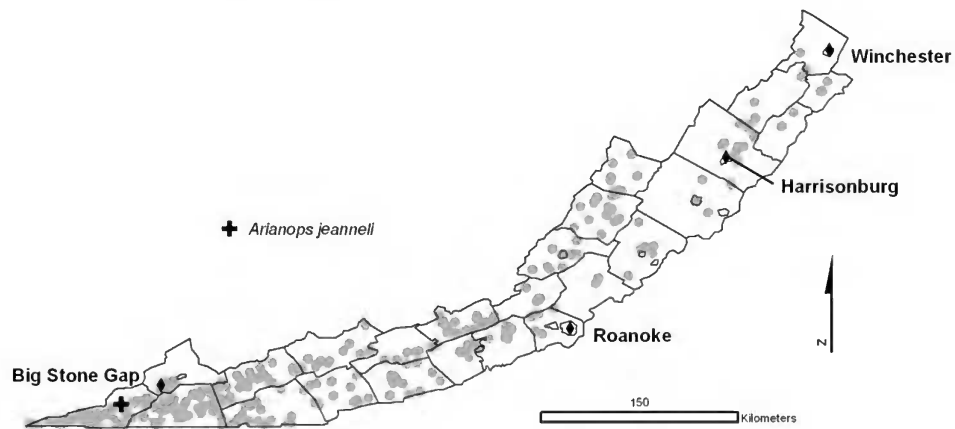


Fig. 46. Distribution of *Arianops jeanneli* in Virginia. Gray dots are all the terrestrial sampling sites.

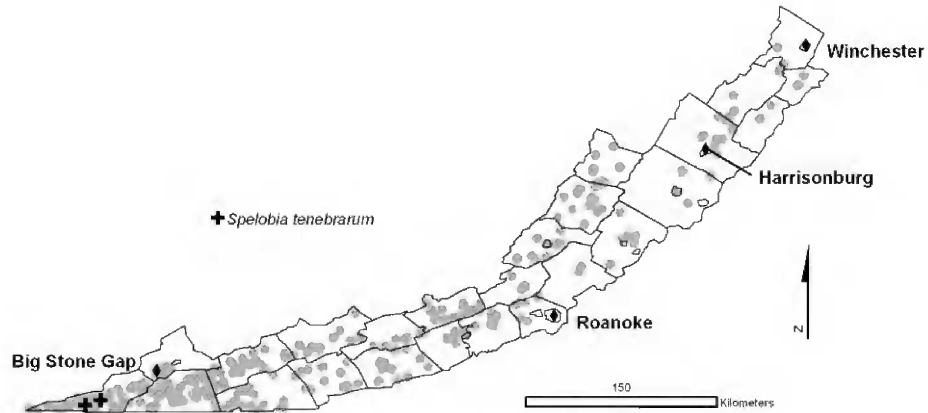


Fig. 47. Distribution of *Spelobia tenebrarum* in Virginia. Gray dots are all the terrestrial sampling sites.

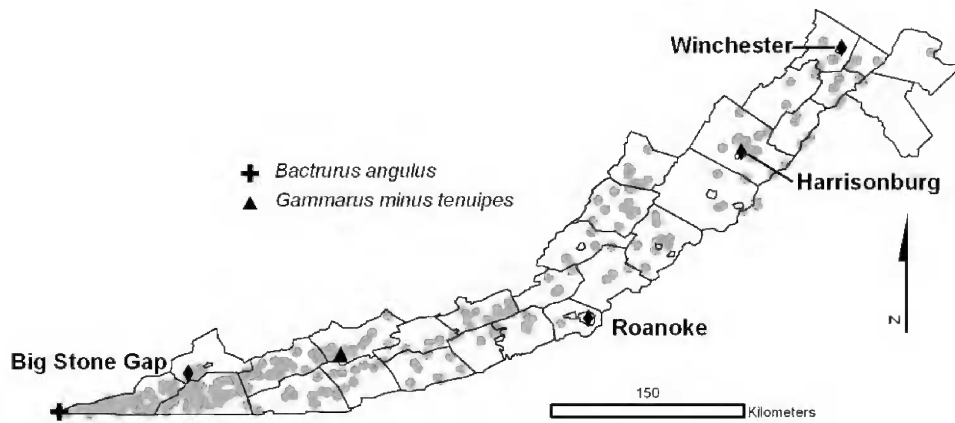


Fig. 48. Distribution of *Bactrurus angulus* and *Gammarus minus* var. *tenuipes* in Virginia. Gray dots are all the aquatic sampling sites.

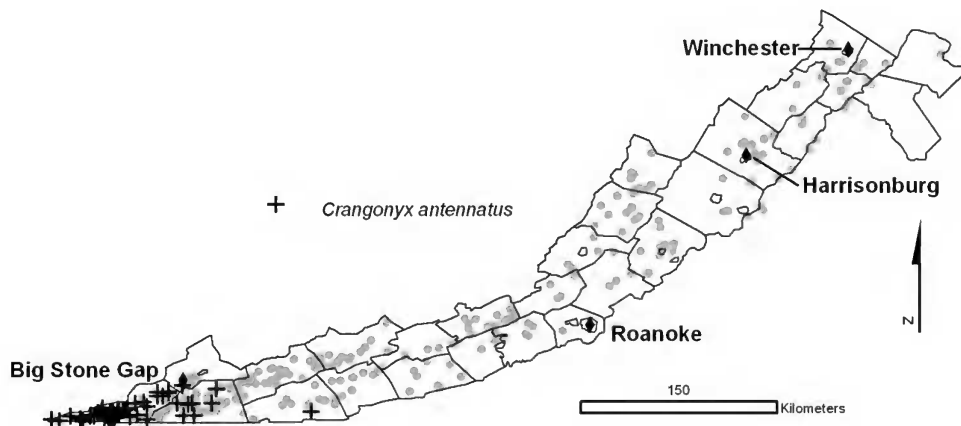


Fig. 49. Distribution of *Crangonyx antennatus* in Virginia. Gray dots are all the aquatic sampling sites.

Crangonyx antennatus Packard 1881

Type Locality: Nickajack Cave, Marion County, Tennessee

Virginia Records (Fig. 49): **Lee Co.:** Baileys Cave, Barney Cave, Bowling Cave, Burial Cave, Cave Springs Cave, Cavin Cave, Cedar Hill Cave, Chances Cave, Combs No. 1 Cave, Cope Cave, Crouse Cave, Cudjo's Cavern (part of the Gap Cave System), Cumberland Saltpetre Cave (part of the Gap Cave System), Flannery Bridge Springs, Frazier Cave, Gallohan No. 1 Cave, Gallohan No. 2 Cave, Garretts Cave, Gibson No. 1 Cave, Gibson-Frazier Cave, Gilliam Cave, Glen Olingers Cave, Golf Course No. 1 Cave, Golf Course No. 2 Cave, Gregorys Cave, Hamblin School Cave, Indian Burial Cave, Jones Saltpetre Cave, Knapper Cave, Lesters Cave, Litton No. 1 Cave, Long Cave, Lucy Beatty Cave, McClure Cave, McCurry Indian Cave, Minors Saltpetre Cave, Molly Wagle Cave, Mount Moriah Pit, Olinger Cave, Reasors Cave, Roadside No. 1 Cave, Seal Cave, Secret Cave, shallow spring in "Cedars", small stream near Sims Spring, Sims Spring Cave, Slemp Cave, Smiths Milk Cave, Spangler Cave, Spout Spring, spring at entrance to Gallohan Cave No. 1, Sweet Potato Cave, Taylor Pit, Thompson Cave, Thompson Cedar Cave, Unthanks Cave, Watsons No. 1 Cave, Young-Fugate Cave; **Scott Co.:** Carters Pit Cave, Daniel Boone Caverns, Daniel Boones Spring, McDavids Cave, Pack Rat Cave, Speers Ferry Cave, Spurlock Cave; **Washington Co.:** Debusk Natural Caverns; **Wise Co.:** Wildcat Cavern Cave, Wildcat Saltpetre Cave.

Remarks: This widespread amphipod is also recorded from caves from eastern Tennessee to northern Alabama.

A total of 21 *Stygobromus* species are found in the study area, 20 from caves, and 16 endemic to the state.

Stygobromus abditus Holsinger 1978

Type Locality: James Cave, Pulaski County, Virginia

Other Virginia Records (Fig. 50): **Giles Co.:** New River Cave; **Montgomery Co.:** Eve Einstein Cave; **Pulaski Co.:** Grindstead Cave, Sam Bells Cave, spring seep/trout pond at New River; **Smyth Co.:** Hillside Hideaway Cave; **Washington Co.:** Dolingers Cave, Ira Miller Cave, Mennick Cave, Red Wolf Cave; **Wythe Co.:** Bertha Cave, Catron Cave, Pierce Mill Cave, Watsons Cave.

Remarks: This species is relatively widespread and common where found.

Stygobromus baroodyi Holsinger 1978

Type Locality: Bathers Cave, Rockbridge County, Virginia

Other Virginia Records (Fig. 50): **Rockbridge Co.:** Bell Cave, Billy Williams Cave, Hottingers Cave, Limekiln Cave, Buck Hill Cave, Grahams Cave, Showalters Cave, Turkey Hill Cave.

Remarks: This species is relatively common and known to date only from Rockbridge County caves.

Stygobromus biggersi Holsinger 1978

Type Locality: Ogdens Cave, Frederick County, Virginia

Other Virginia Records (Fig. 50): **Clarke Co.:** well on farm near Boyce; **Frederick Co.:** Johns Cave, monitoring well and test well near Stephens City; **Loudoun Co.:** Rust Cave No. 1; **Warren Co.:** Brother Daves Cave.

Remarks: Other localities, north and northeast of Virginia, include sites (caves and wells) in Jefferson and Berkeley counties, West Virginia, Washington Co., Maryland, and Cumberland and Franklin counties, Pennsylvania.

Stygobromus conradi (Holsinger 1967)

Type Locality: Breathing Cave, Bath County, Virginia

Other Virginia Records (Fig. 51): **Bath Co.:** Barberry Cave, Bobcat Cave, Butler Cave, Mountain Grove Cave, Serpent Cave, Starr Chapel Cave; **Highland Co.:** Aqua Cave, Bullpasture Mountainside Cave, Huppmans Saltpetre Cave, Huppmann Jr. Cave, Marshalls Cave, Helictite Cave, Water Sinks Cave.

Stygobromus cumberlandus Holsinger 1978

Type Locality: Wildcat Saltpetre Cave, Wise County, Virginia

Other Virginia Records (Fig. 51): **Lee Co.:** Baileys Cave, Cliff Cave, Indian Cave; **Scott Co.:** well near Duffield; **Wise Co.:** Kelly Cave, Parsons Cave, Rocky Hollow Cave.

Remarks: This species is relatively widespread and recorded from caves and a water well in the 3-county area of Lee, Scott, and Wise counties in far southwestern Virginia.

Stygobromus ephemerus (Holsinger 1969)

Type Locality: Tawneys Cave, Giles County, Virginia

Other Virginia Records (Fig. 51): **Giles Co.:** Canoe Cave, Stay High Cave.

Remarks: As presently known, this species has a very limited distribution, and the majority of collections to date have been from Tawneys Cave.

Stygobromus estesi Holsinger 1978

Type Locality: Rufe Caldwell Cave, Craig County, Virginia

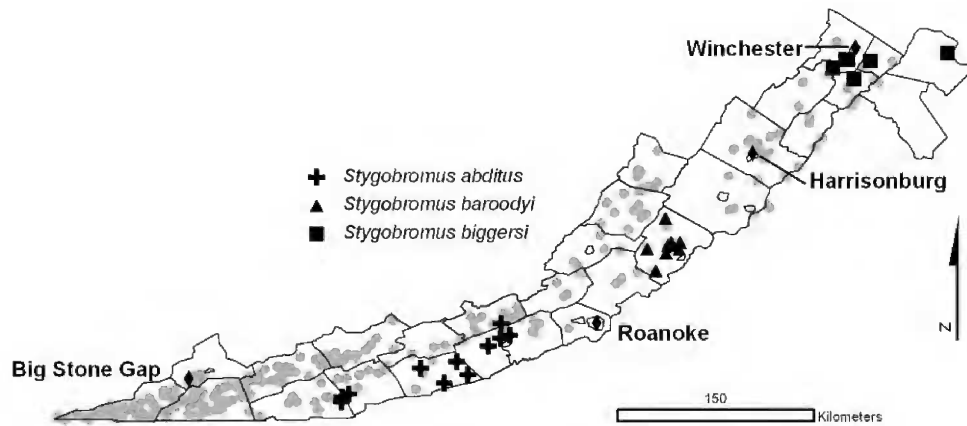


Fig. 50. Distribution of *Stygobromus abditus*, *S. baroodyi*, and *S. biggersi* in Virginia. Gray dots are all the aquatic sampling sites.

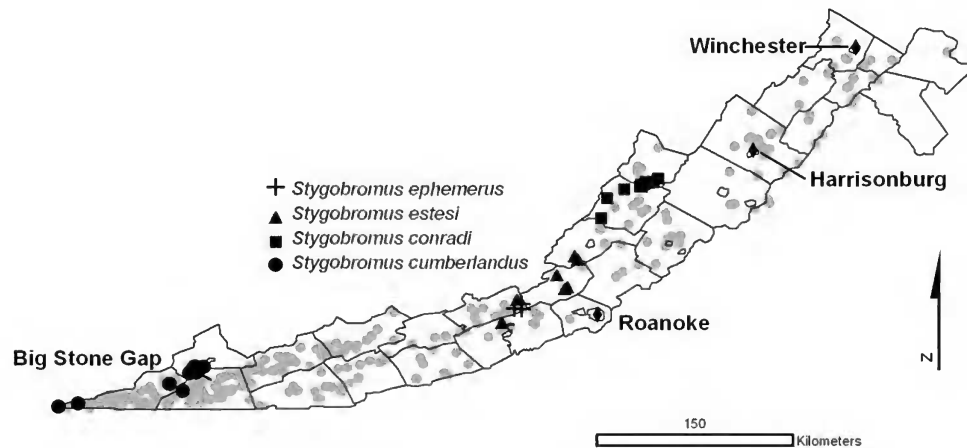


Fig. 51. Distribution of *Stygobromus conradi*, *S. cumberlandus*, *S. ephemerus*, and *S. estesi* in Virginia. Gray dots are all the aquatic sampling sites.

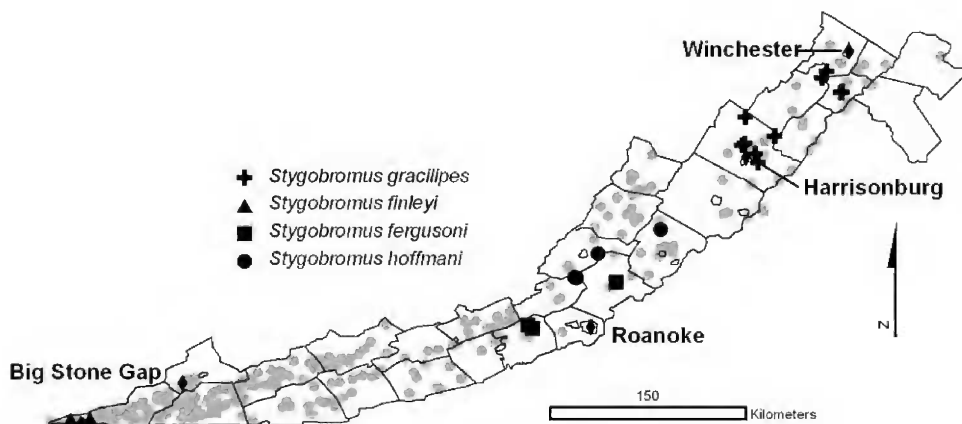


Fig. 52. Distribution of *Stygobromus fergusoni*, *S. finleyi*, *S. gracilipes*, and *S. hoffmani* in Virginia. Gray dots are all the aquatic sampling sites.

Other Virginia Records (Fig. 51): **Alleghany Co.**: Arritt Mill Tunnel Cave, Paxtons Cave; **Craig Co.**: Newcastle Murder Hole, Shires Saltpetre Cave; **Giles Co.**: spring on tributary of Johns Creek; **Montgomery Co.**: spring in Poverty Hollow and seeps at old mine drainage near McCoy.

Remarks: This species is recorded from a variety of groundwater habitats, including caves, springs, seeps, and mine drainage.

Stygobromus fergusonii Holsinger 1978

Type Locality: Slussers Chapel Cave, Montgomery County, Virginia

Other Virginia Records (Fig. 52): **Botetourt Co.**: Karls Pit Cave; **Montgomery Co.**: Old Mill Cave.

Remarks: This species is recorded primarily from seep pools in three caves.

Stygobromus finleyi Holsinger 1978

Type Locality: English Cave, Claiborne County, Tennessee

Virginia Records (Fig. 52): **Lee Co.**: Cavin Cave, Indian Burial Cave, Jones Saltpetre Cave, Longs Cave.

Remarks: This species is recorded from a few caves in the Powell Valley of southwestern Virginia and northeastern Tennessee where it is usually found in drip pools.

Stygobromus gracilipes (Holsinger 1967)

Type Locality: Skyline Caverns, Warren County, Virginia

Other Virginia Records (Fig. 52): **Clarke Co.**: well on John Staelin farm and well on Greenwood farm; **Frederick Co.**: Ogdens Cave; **Page Co.**: Woods Cave; **Rockingham Co.**: Church Mountain Cave, Deer Hole (cave), Devil's Hole (cave), Endless Caverns, Massanutten Caverns, 3-D Maze Cave; **Shenandoah Co.**: Crystal Cave; **Warren Co.**: Allens Cave, Brother Daves Cave, Front Royal Caverns.

Remarks: This species is also recorded from caves and wells north and northeast of Virginia in Berkeley and Jefferson counties, West Virginia; a spring in Washington Co., Maryland; and Needy Cave in Franklin Co., Pennsylvania.

Stygobromus hoffmani Holsinger 1978

Type Locality: Lowmoor Cave, Alleghany County, Virginia

Other Virginia Records (Fig. 52): **Alleghany Co.**: McElwee Cave; **Craig Co.**: small spring with culvert under road near Bald Mountain; **Rockbridge Co.**: seep in Goshen Wildlife Management Area.

Remarks: This species has been collected from a variety of groundwater habitats in the three Virginia counties

listed.

Stygobromus hubbardi Holsinger 2009

Type Locality: Battlefield Crystal Cave (Crystal Caverns at Hupps Hill), Shenandoah County, Virginia

Other Virginia Record (Fig. 53): **Shenandoah Co.**: Keyhole Cave.

Remarks: This tiny, rare species (ca. 1.7-2.3 mm in length) has been collected to date from tiny drip pools in the two caves listed above.

Stygobromus interitus Holsinger 1978

Type Locality: New Castle Murder Hole Cave, Craig County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 53).

Remarks: A very rare species known only on the basis of two female specimens.

Stygobromus leensis Holsinger 1978

Type Locality: Litton No. 1 Cave, Lee County, Virginia

Other Virginia Records (Fig. 53): **Lee Co.**: Gallohan No. 2 Cave, Skull Cave.

Remarks: To date, this species is recorded from drip/seep pools in three caves in central Lee County.

Stygobromus mackini Hubricht 1943

Type Locality: Sikes Cave, Russell County, Virginia

Other Virginia Records (Fig. 54): **Bland Co.**: Becky Knob Cave, Buddy Penleys Cave, Cedar Cliff Saltpetre Cave, Gollehorn Cave, Hamilton Cave, Newberry-Banes Cave, Repass Saltpetre Cave, Spring Hollow Cave; **Giles Co.**: Ballards Cave, Birthday Cave, Colby Cave, Doe Mountain Cave, Giant Caverns, New River Cave, Salamander Cave, spring at Bear Cliff near Mountain Lake, spring along small tributary to Johns Creek, Spruce Run Mountain Cave, Starnes Cave, Stay High Cave, Straleys Cave, Tawneys Cave; **Lee Co.**: Cave Road Cave, Fisher Cave; **Russell Co.**: Austines Hilltop Cave, Banners Corner Cave, Bundys No. 2 Cave, Burns Handline Cave, Bush Handline Cave, Concrete Tank Cave, Densmore Hill Cave, Dickenson Cave, Dorton Spring Cave, Grays Cave, Jessie Cave, Johnson Cave, Munsey Cave, Porgie Bundys Cave, Riverbend Cave, Rocky Fork Cave, Sikes Cave, Smiths Drop Cave, Trooper Said Cave; **Scott Co.**: Abrams Cave, Big Spiders in a Little Maze Cave, Blair-Collins Cave, Blowing Hole Cave, Bolling Cave, Cave Hollow Cave, Contact Cave, Deep Spring Cave, Fields Cave, Flannery Cave, Fugate Cave, Greears Sweet Potato Cave, Grigsby Cave, Hill Cave, Hillman Cemetery Pit Cave, Jack Cave, Jackson Cave, Jessee Branch Cave, Kerns Smoke-Hole Cave, Lane Cave, Little Duck Cave,

McDavids Cave, McNew Cave, Moccasin Valley Cave, Natural Tunnel Cave, Pack Rat Cassel Cave, Pond Cave, Queens Cave, Rhoton Milk and Butter Cave, Speers Ferry Cave, Spurlock Cave, Taylor No. 1 Cave, Taylor No. 2 Cave, Winding Stair Cave, Wolfe Cave; **Smyth Co.:** Big Sink Cave, Buchanan Saltpetre Cave, Hancock Cave, Harmon Cave, Little Saltpetre Cave, McMullin Cave, Tilson Saltpetre Cave, Walkers Cave, Worleys Cave; **Tazewell Co.:** Cauliflower Cave, Chimney Rock Cave, Corkscrew Cave, Crocketts Cave, Fallen Rock Cave, Glenwood Church Cave, Higginbothams No. 1 Cave, Hugh Young Cave, Little River Cave, Lost Mill No. 1 Cave, Martins Cave, small spring on east slope of Beartown Mountain, Steeles Cave, Ward Cove Cave; **Washington Co.:** Ball Battery Cave, covered spring 1 mile NW of Court House, Singleton Cave, Substation Cave, Thunder Cave; **Wise Co.:** Big Kelly Cave, Blowing Cave, Omega Cave System, Parsons Cave, Wildcat Saltpetre Cave.

Remarks: *Stygobromus mackini* is clearly the most common and widespread stygobiotic species in Virginia. It is also recorded from seven caves in neighboring West Virginia, including five in Mercer County and two in Monroe County (Fong et al., 2007), as well as nine caves in seven counties of upper East Tennessee (Holsinger, 1978; Holsinger & Culver, 1988; J.R. Holsinger, unpub. data). In addition, this species or a morphologically very closely similar species is recorded from a cave in Charlestown in Clark Co., Indiana, and at least five caves in eastern Kentucky. However, the populations in Indiana and Kentucky need further study before their taxonomic relationship with *S. mackini* s. str. can be determined.

Stygobromus mausi Holsinger 2009

Type Locality: Round Hill Cave, Rockingham County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 53).

Remarks: To date, this tiny, rare species is known only from nine specimens collected from a single drip pool in the type locality.

Stygobromus morrisoni (Holsinger 1967)

Type Locality: Witheros Cave, Bath County, Virginia

Other Virginia Records (Fig. 54): **Bath Co.:** Crossroads Cave, Clarks Cave; **Highland Co.:** Corbett Cave, Secret Anthodite Cave.

Remarks: The range of this species extends north-northeast into West Virginia where it has been collected from Dyers Cave in Hardy Co. and Kenny Simmons Cave in Pendleton Co. (Fong et al., 2007).

Stygobromus mundus (Holsinger 1967)

Type Locality: Witheros Cave, Bath County, Virginia

Other Virginia Records (Fig. 55): **Alleghany Co.:** tributary to Cowpasture River; **Bath Co.:** Porters Cave, Russells Reserve Cave, Williams Cave.

Remarks: This species is fairly common in small streams but is more often collected from drip pools. As noted above, it was also collected once from a surface stream, presumably flushed out of a nearby subterranean habitat.

Stygobromus pseudospinosus Holsinger 1978

Type Locality: Luray Caverns, Page County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 55).

Remarks: This species is known only from drip pools in Luray Caverns. Both *S. pseudospinosus* and *S. spinosus* are morphologically closely similar and may well be conspecific despite being considered separate species by Holsinger (1978). A resolution of this question awaits a DNA analysis.

Stygobromus spinosus (Hubricht & Mackin 1940)

Type Locality: spring near Hawksbill Mountain on Skyline Drive, Madison County, Virginia

Other Virginia Records (Fig. 55): **Albemarle Co.:** spring in Saddle Hollow; spring 2.1 km SE of Sawmill Ridge Overlook in Shenandoah National Park; **Clarke Co.:** seep at Reservoir Hollow on Appalachian Trail; **Fauquier Co.:** seeps in Wildcat Hollow, G. Richard Thompson Wildlife Management Area; **Greene Co.:** spring at Swift Run Gap, Skyline Drive, Shenandoah National Park; spring near Pinefield Shelter, Shenandoah National Park; **Nelson Co.:** Old Afton Railroad Tunnel; **Page Co.:** 3.2 km S of Big Meadows, Skyline Drive; **Rappahannock Co.:** spring at Indian Run Shelter, Shenandoah National Park; **Warren Co.:** seep in woods near Blue Mountain; spring near Browntown Valley Overlook, Shenandoah National Park.

Remarks: This is widely distributed in small springs and seeps, and is the only *Stygobromus* species in this study not to be found in caves. The habitat is under-collected relative to caves, and there are likely many more populations. Together with *S. obrutus* (see Culver et al., 2012a), it is outside the range of all other described *Stygobromus*.

Stygobromus stegerorum Holsinger 1978

Type Locality: Madison Saltpetre Cave, Augusta County, Virginia

Other Virginia Records (Fig. 55): **Augusta Co.:** Blue Hole Cave, Stegers Fissure.

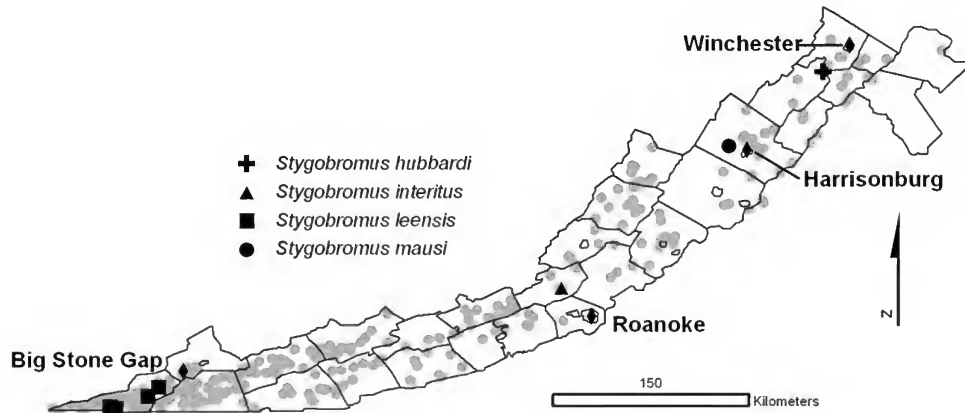


Fig. 53. Distribution of *Stygobromus hubbardi*, *S. interitus*, *S. leensis*, and *S. mausi* in Virginia. Gray dots are all the aquatic sampling sites.

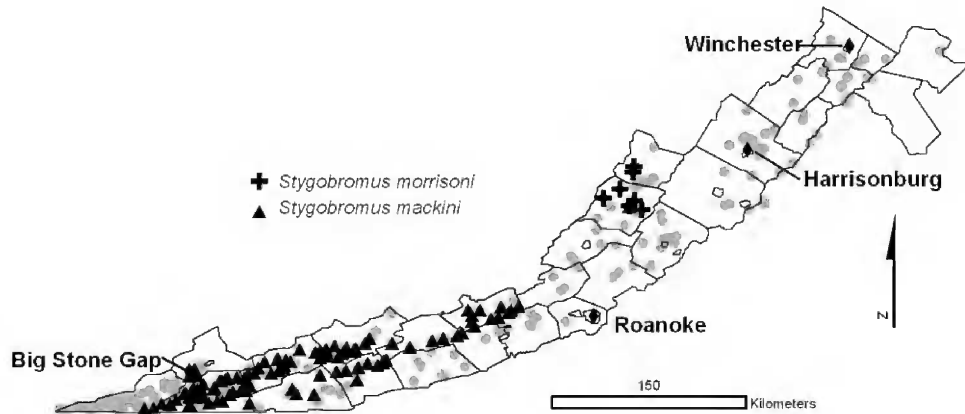


Fig. 54. Distribution of *Stygobromus mackini* and *S. morrisoni* in Virginia. Gray dots are all the aquatic sampling sites.

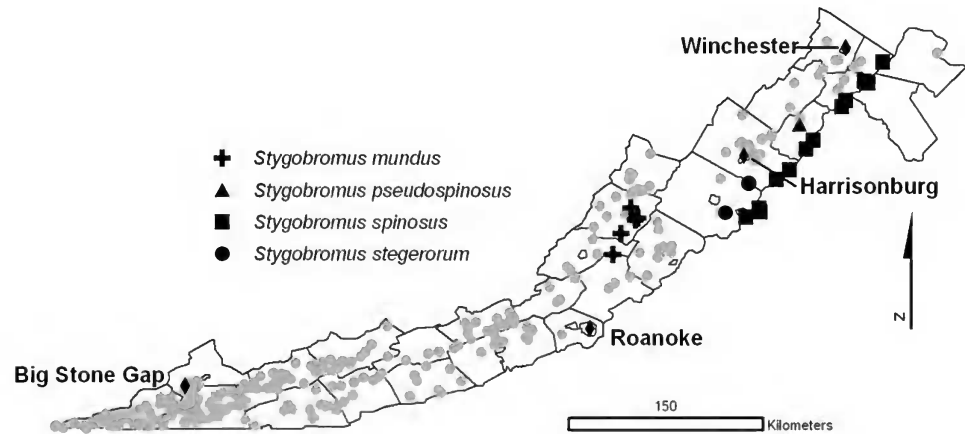


Fig. 55. Distribution of *Stygobromus mundus*, *S. pseudospinosus*, *S. spinosus*, and *S. stegerorum* in Virginia. Gray dots are all the aquatic sampling sites.

Remarks: To date, this species has been recorded from deep, phreatic lakes in the caves listed above. All of these lakes are also inhabited by the troglomorphic cirolanid isopod *Antrolana lira* Bowman. This species is listed as State Endangered.

Family Gammaridae

Gammarus minus var. *tenuipes* Shoemaker 1940

Type Locality: Organ Cave, Greenbrier County, West Virginia

Virginia Records (Fig. 48): **Tazewell Co.**: Fallen Rock Cave, Gillespie Water Cave, Hugh Young Cave.

Remarks: See Fong et al. (2007) for the details of a study of this morphologically similar variety in a karst basin of Greenbrier and Monroe counties in southern West Virginia. It is assumed that the variety *G. minus* var. *tenuipes* has evolved at least twice and independently under similar selection pressures, resulting in a morphologically similar form “*tenuipes*” in two completely separate karst basins: one in southern West Virginia and the other in Tazewell Co., Virginia.

Order Isopoda

Family Asellidae

Caecidotea bowmani Lewis 1980

Type Locality: Natural Bridge Park, drain on trail, Rockbridge County, Virginia

Other Virginia Record (Fig. 56): **Botetourt Co.**: Purgatory Cave.

Remarks: The Purgatory Cave record is an addition to the Natural Bridge Park record noted by Lewis (2009). This isopod occupies both shallow subterranean habitats and caves.

Caecidotea cumberlandensis Lewis 2000

Type Locality: Indian Cave, Lee County, Virginia

Other Virginia Record (Fig. 56): **Lee Co.**: Cliff Cave.

Remarks: Known only from two neighboring caves in extreme southwestern Virginia.

Caecidotea henroti (Bresson 1955)

Type Locality: Smokehole Cave, Giles County, Virginia

Other Virginia Records (Fig. 56): **Giles Co.**: Tawneys Cave; **Nelson Co.**: Old Afton Railroad Tunnel; **Pulaski Co.**: James Cave.

Remarks: Known from four sites, including an abandoned railroad tunnel.

Caecidotea holsingeri (Steeves 1963)

Type Locality: Organ Cave, Greenbrier County, West

Virginia

Virginia Records (Fig. 56): **Alleghany Co.**: Paxtons Cave; **Bath Co.**: Barberry Cave, Breathing Cave, Butler-Sinking Creek Cave, Cave Run Pit Cave, Clarks Cave; **Giles Co.**: Spring on small tributary of Johns Creek; **Highland Co.**: Aqua Cave, Helictite Cave, Sweet Anthodite Cave.

Remarks: This is a widespread species found in caves and occasionally surface streams in karst areas in parts of Virginia, West Virginia, and Maryland (Fong et al., 2007).

Caecidotea incurva (Steeves & Holsinger 1968)

Type Locality: Berry Cave, Roane County, Tennessee

Virginia Records (Fig. 57): **Smyth Co.**: McMullin Cave; **Washington Co.**: Dolingers Cave; **Wythe Co.**: Bowles Spring Cave, Deep Spring Cave, Early Cave, Gardners Cave, Groseclose Cave No. 1, Lone Ash No. 2 Cave, Mockleys Cave.

Remarks: This species also occurs in Blount County, Tennessee.

Caecidotea mausi Lewis 2009

Type Locality: Brother Daves Cave, Warren County, Virginia

Other Virginia Records: Known in Virginia only from the type locality (Fig. 58).

Remarks: This species is also known from several sites in Maryland.

Caecidotea pricei Levi 1949

Type Locality: Refton Cave, Lancaster County, Pennsylvania

Virginia Records (Fig. 57): **Augusta Co.**: Barterbrook Spring Cave, Glade Cave; **Bath Co.**: Butler-Sinking Creek Cave; **Frederick Co.**: Ogdens Cave; **Loudoun Co.**: Rust Cave; **Page Co.**: Will Mauck Cave; **Rockbridge Co.**: Bathers Cave, Bell Cave, Billy Williams Cave, Hottinger Cave, Showalters Cave, Tolleys Cave; **Rockingham Co.**: Ann Millers Cave, Cedar Hill Cave, Endless Cave, Massanutten Caverns, Mauzy Spring, Stonewall's Spring; **Shenandoah Co.**: Flemings Cave; **Warren Co.**: Skyline Caverns, Water Hole Cave.

Remarks: This species is at the southernmost portion of its range in Virginia. It is also known from West Virginia, Maryland, and Pennsylvania.

Caecidotea recurvata (Steeves 1963)

Type Locality: Unthanks Cave, Lee County, Virginia

Other Virginia Records (Fig. 58): **Lee Co.**: Baileys Cave, Barney Cave, Bowling Cave, Burial Cave, Cattle Cave, Cave Springs Cave, Combs No. 1 Cave, Cope Cave, Crouse Cave, Earlys Cave, Fisher Cave,

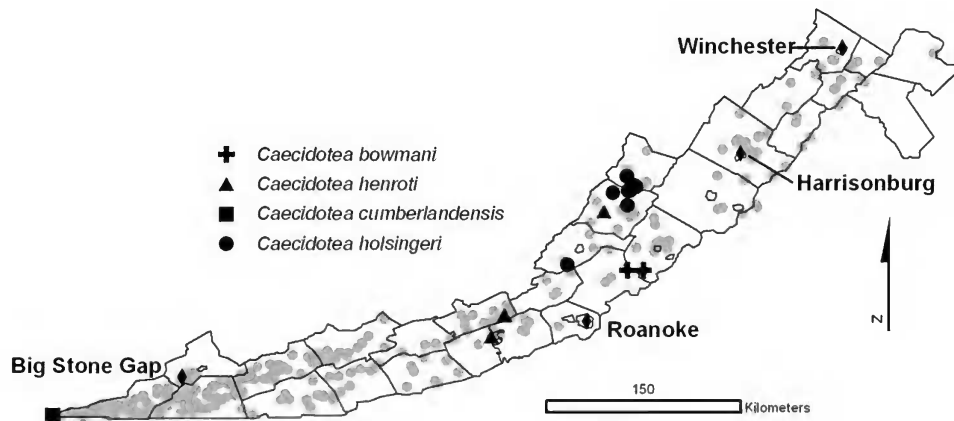


Fig. 56. Distribution of *Caecidotea bowmani*, *C. cumberlandensis*, *C. henroti*, and *C. holsingeri* in Virginia. Gray dots are all the aquatic sampling sites.

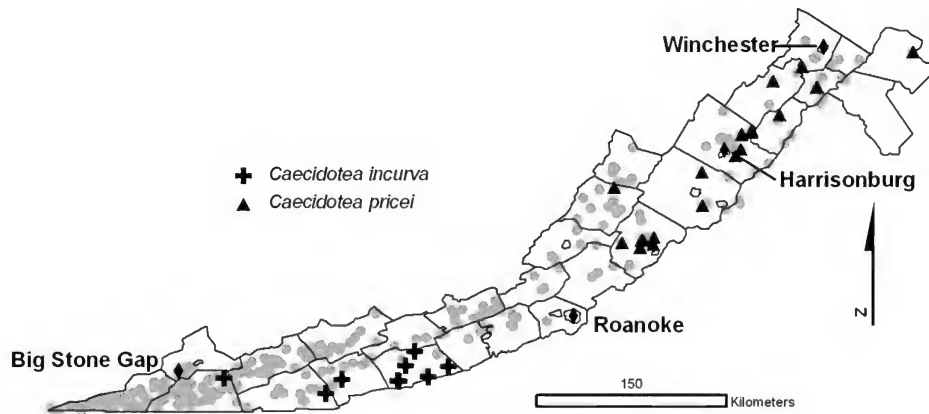


Fig. 57. Distribution of *Caecidotea incurva* and *C. pricei* in Virginia. Gray dots are all the aquatic sampling sites.

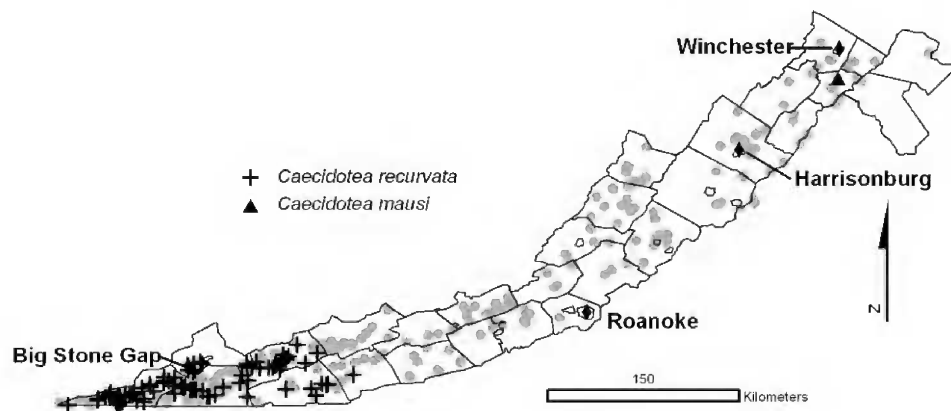


Fig. 58. Distribution of *Caecidotea mausi* and *C. recurvata* in Virginia. Gray dots are all the aquatic sampling sites.

Gallohan No. 1 Cave, Gallohan No. 2 Cave, Gibson No. 1 Cave, Gilley Cave, Gilliam Cave, Golf Course No. 1 Cave, Golf Course No. 2 Cave, Hamblin School Cave, Kinzer Hollow Cave, Knapper Cave, Litton No. 1 Cave, Long Cave, McClure Cave, McCurry Indian Cave, Minors Saltpetre Cave, Molly Wagle Cave, Olinger Cave, Reasors Cave, Roadside No. 1 Cave, Seal Cave, Secret Cave, Skull Cave, Smiths Milk Cave, Spangler Cave, Sweet Potato Cave, Tater Cave, Taylor Pit Cave, T-Bone Cave, Thompson Cedar Cave, Young-Fugate Cave; **Russell Co.:** Banners Corner Cave, Big Spring Cave, Breeding Cave, Bundys No. 2 Cave, Bundys Pearl Cave, Burns Cave, Concrete Tank Cave, Daugherty Cave, Dickerson Cave, Dorton Spring Cave, Grays Cave, Indian Cave, Jessie Cave, Johnson Cave, Munsey Cave, Phreatic To A Fault Cave, Porgie Bundys Cave, Seven Springs Cave, Smiths Cave, Stewart Monks Cave, Sykes Cave; **Scott Co.:** Blair-Collins Cave, Bob Dean Cave, Coley No. 2 Cave, Contact Cave, Flannery Cave, Jack Cave, Jesse Branch Cave, Lane Cave, McDavids Cave, Rhoton Milk and Butter Cave, Spurlock Cave, Sweet Potato Cave, Taylor No. 1 Cave, Taylor No. 2 Cave, Thomas Smith Cave, Triplet Wells Cave; **Smyth Co.:** McMullin Cave; **Washington Co.:** Brass Kettle Hole, Cave Spring Cave, David Debusk Cave, Debusk Mill No. 1 Cave, Fraleys Cave, Thunder Cave; **Wise Co.:** Bloomer Cave, Burtons Cave, Hairy Hole Cave, Kelly Cave, Little Kennedy Cave, Parsons Cave, Rocky Hollow Cave, Wildcat Saltpetre Cave.

Remarks: Found in caves and karst springs in Virginia and Tennessee. This species can be found in drip pools and streams within caves.

Caecidotea richardsonae Hay 1901

Type Locality: Nickajack Cave, Marion County, Tennessee

Virginia Records (Fig. 59): **Lee Co.:** Gregorys Cave, Olinger Cave, Smiths Milk Cave; **Russell Co.:** Cascade Pit Cave; **Scott Co.:** Blair-Collins Cave, Hortons Cave, Moccasin Valley Cave, Speers Ferry Cave, Wolfe Cave; **Tazewell Co.:** Bowens Cave, Fallen Rock Cave, Hugh Young Cave, Little River Cave, Lost Mill No. 3 Cave, Rosenbaums Water Cave, Stonley Cave; **Washington Co.:** Walker Mountain Saltpetre Cave.

Remarks: This species co-occurs with *C. recurvata* at a few caves, and shares a similar range.

Caecidotea vandeli (Bresson 1955)

Type Locality: Erhart Cave, Montgomery County, Virginia

Other Virginia Records (Fig. 59): **Alleghany Co.:** Falling Spring Creek Cave; **Bath Co.:** Blowing Cave; **Botetourt Co.:** Brough Cave No. 2; **Craig Co.:** Rufe

Caldwell Cave; **Giles Co.:** New River Cave, Spruce Run Mountain Cave, Stay High Cave; **Montgomery Co.:** Aunt Nellies Hole Cave, Old Mill Cave, Slussers Chapel Cave; **Roanoke Co.:** Goodwins Cave; **Shenandoah Co.:** Barb Cave; roadside seeps along Short Mountain.

Remarks: The type locality was destroyed by quarrying. This species also occurs in Maryland, where it has been recorded from several springs and a mine (Lewis et al., 2011).

Lirceus culveri Estes & Holsinger 1976

Type Locality: McDavids Cave, Scott County, Virginia

Other Virginia Records (Fig. 60): **Scott Co.:** Carters Pit Cave, Fugate Cave, Jackson Cave.

Remarks: This species is apparently endemic to a single karst spring basin in the Rye Cove area of Scott County. It is typically found on and among small to medium-sized rocks in shallow portions of streams.

Lirceus usdagalun Holsinger & Bowman 1973

Type Locality: Gallohan No. 1 Cave, Lee County, Virginia

Other Virginia Records (Fig. 60): **Lee Co.:** Flannery Bridge Springs, Gallohan No. 2 Cave, Golf Course No. 2 Cave, Masons Cave, Sims Creek Springs, Surgener Cave, Thompson Cedar Cave.

Remarks: A Virginia endemic, this species is listed as Endangered by the U.S. Fish and Wildlife Service. It is restricted to a handful of shallow cave systems in the Cedars area of Lee County.

Family Cirolanidae

Antrolana lira Bowman 1964

Type Locality: Madison Saltpetre Cave, Augusta County, Virginia

Other Virginia Records (Fig. 61): **Augusta Co.:** Blue Hole Cave, Stegers Fissure; **Clarke Co.:** well at Meade Church; **Rockbridge Co.:** Limekiln Cave; **Rockingham Co.:** 3-D Maze Cave, Devils Hole Cave, Linville Quarry No. 3 Cave, Massanutten Caverns; **Warren Co.:** Brother Daves Cave, Front Royal Caverns Cave, Power Plant Pit Cave.

Remarks: For thirty years, this unique species was known only from a single isolated, groundwater aquifer (Holsinger & Culver, 1988). It is now known from deep groundwater aquifers in the Shenandoah Valley of Virginia and West Virginia (Holsinger et al., 1994; Fong et al., 2007), and these populations exhibit considerable genetic variation (Hutchins et al., 2010). Globally, stygobiotic cirolanids are found in areas with a past connection to marine waters. The presence of

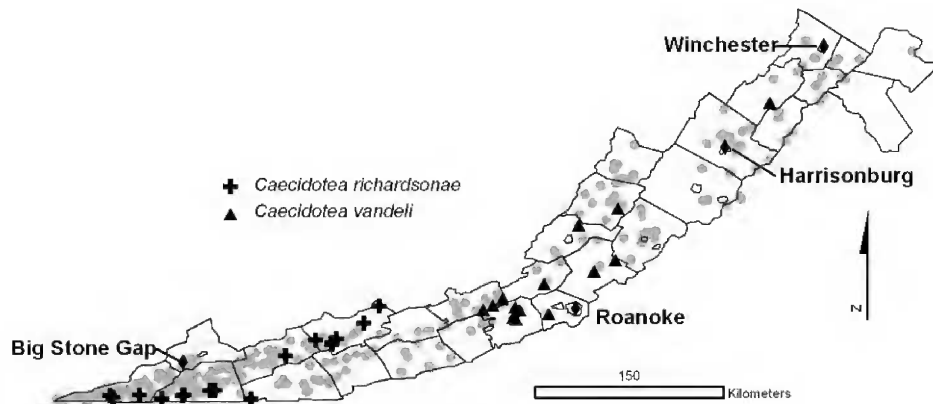


Fig. 59. Distribution of *Caecidotea richardsonae* and *C. vandeli* in Virginia. Gray dots are all the aquatic sampling sites.

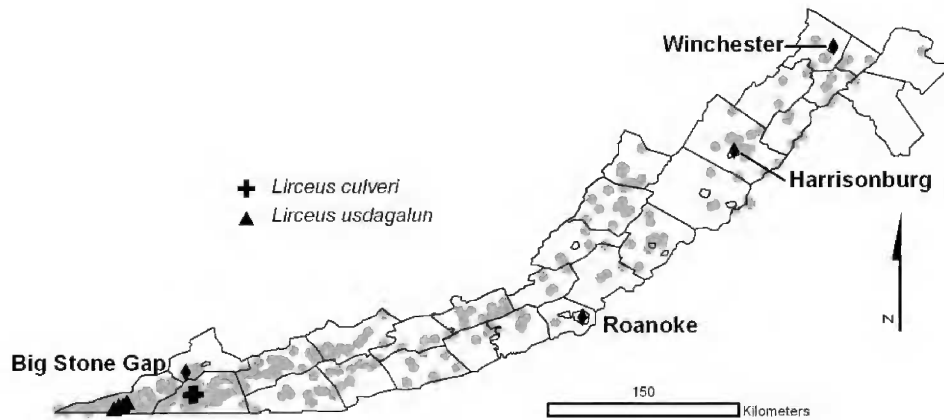


Fig. 60. Distribution of *Lirceus culveri* and *L. usdagalun* in Virginia. Gray dots are all the aquatic sampling sites.

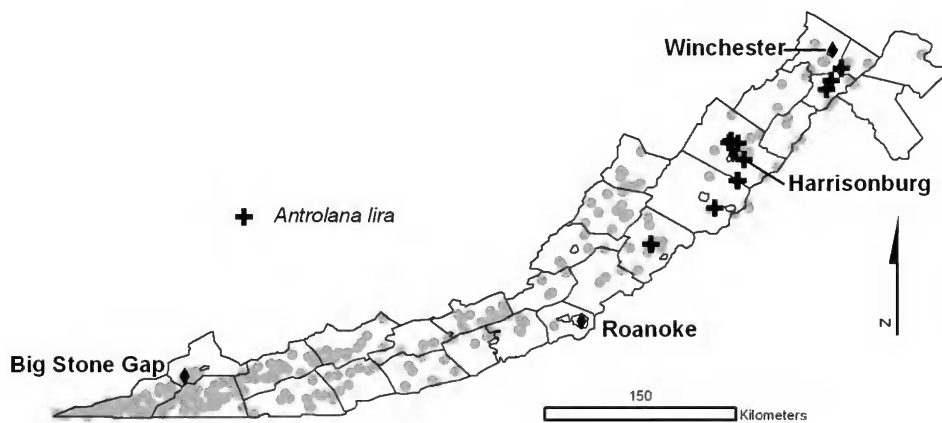


Fig. 61. Distribution of *Antrolana lira* in Virginia. Gray dots are all the aquatic sampling sites.

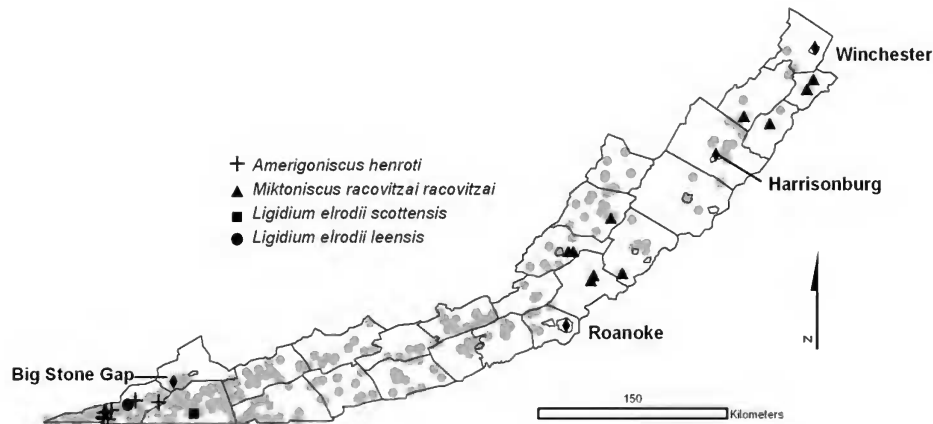


Fig. 62. Distribution of *Amerigoniscus henroti*, *Ligidium elrodii leensis*, *L. e. scottensis*, and *Miktoniscus racovitzai racovitzai* in Virginia. Gray dots are all the terrestrial sampling sites.

A. lira in the Shenandoah Valley implies that such a past connection existed here. It is listed as Threatened by the U.S. Fish and Wildlife Service.

Family Ligiidae

Ligidium elrodii leensis Schultz 1970

Type Locality: Bowling Cave, Lee County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 62).

Remarks: *L. elrodii* is a wide-ranging, surface-dwelling isopod in the eastern U.S. and Canada. This subspecies is slightly troglomorphic and lives on wet organic debris.

Ligidium elrodii scottensis Schultz 1970

Type Locality: Coley Cave No. 2, Scott County, Virginia

Other Virginia Records: Known only from the type locality (Fig. 62)

Remarks: This subspecies is slightly troglomorphic and lives on wet organic debris.

Family Trichoniscidae

Amerigoniscus henroti Vandel 1950

Type Locality: Gilley Cave, Lee County, Virginia

Other Virginia Records (Fig. 62): **Lee Co.:** Cope Cave, Earlys Cave, Gallohan No. 1 Cave, Kinzer Hollow Cave, Smiths Milk Cave, Spangler Cave, Sweet Potato Cave, Unthanks Cave.

Miktoniscus racovitzai racovitzai Vandel 1965

Type Locality: Luray Caverns, Page County, Virginia

Other Virginia Records (Fig. 62): **Alleghany Co.:** Island Ford Cave, Lowmoor Cave; **Bath Co.:** Russells Reserve Cave; **Botetourt Co.:** Karls Pit, Peerys Saltpetre Cave; **Rockbridge Co.:** Buck Hill Cave; **Shenandoah Co.:** Shenandoah Caverns; **Warren Co.:** Allens Cave, Brother Daves Cave.

Remarks: This subspecies was also reported from Slacks Cave in Scott Co., Kentucky (Vandel, 1965). A second subspecies, *M. r. oklahomensis*, is found in one cave in Oklahoma. Given the great distances separating these populations, they may be separate species.

DISCUSSION

There are many ways, lengthy though it is, that this list of species is incomplete. The limitation of the list to only troglobionts, even when morphologically unmodified species limited to subterranean habitats are included, does not encompass all species with reproducing populations in caves. Graening et al. (2011) listed over 1,300 species found in caves in Arkansas and Oklahoma, yet less than ten percent of these are troglobionts and stygobionts. While many of the species listed by these authors are accidentals or temporary visitors, there are a number of ecologically important species in Arkansas and Oklahoma caves that are troglophiles and stygophiles. The same holds for Virginia caves. Holsinger & Culver (1988) discussed some of these, but there needs to be an up-to-date

treatment.

There are also undescribed and/or undiscovered stygobionts and troglobionts in Virginia. The number of undiscovered species can be estimated if multiple samples of the same habitat are available (e.g., Schneider & Culver, 2004), but this technique has not been applied to the Virginia cave fauna. What is known is that there are a number of undescribed species that have been collected. This is particularly true for beetles in the genus *Pseudanophthalmus* (Barr, 2004) and diplurans in the genus *Litocampa*, where undescribed species have been known since Holsinger & Culver's (1988) monograph. Some of the microfauna and some habitats (especially epikarst) have hardly been collected at all, but likely are relatively rich in species (see Pipan & Culver [2005] for an example from a West Virginia cave).

The topics of biogeography and ecology of subterranean animals have not been covered in this report, but we hope that the data presented here will provide a stimulus for analytical studies in these fields. Little work has been done on phylogeography (e.g., Hutchins et al., 2010) and a quantitative analysis of species richness patterns (see Zagamajster et al. [2010] for some techniques) is also desirable.

Finally, we note that much of the Virginia cave fauna may be at risk of extinction, both because of the restricted ranges of nearly all species (many are single cave endemics) and because relatively few caves, their surface area footprints, and their recharge areas are protected. The bright spots are both NGOs such as The Nature Conservancy, Virginia Speleological Survey, Cave Conservancy of the Virginias, Appalachian Cave Conservancy (formerly Perkins Cave Conservancy), Butler Cave Conservation Society, West Virginia Cave Conservancy (which owns caves in Virginia as well), and the Mid-Atlantic Karst Conservancy, and government agencies, especially the Virginia Department of Conservation and Recreation's Natural Heritage Program and the Virginia Department of Game and Inland Fisheries. All have been active in protecting Virginia caves. The U.S. Fish and Wildlife Service continues to fund numerous projects in Virginia related to the study of listed trogllobiotic and stygobiotic species, the implementation of best management practices on private lands to protect these species, and the acquisition of critical habitat for long-term protection. In addition, there is a Virginia Cave Board appointed by the governor which acts as an information source and provides guidance with respect to cave and karst protection. The Virginia Cave Protection Act of 1979 established the Cave Board, and also specifies criminal penalties for cave vandalism, sale of cave formations, and unpermitted scientific collections,

while shielding landowners from liability when allowing access to caves.

ACKNOWLEDGEMENTS

We are grateful to many colleagues who have assisted us in recent years in various phases of the present study, including advice, new descriptions, species determinations, and useful data from their own collections. An older listing pertaining to a previous study can be found in Holsinger & Culver (1988). We apologize to anyone who might have been inadvertently omitted: Thomas C. Barr, Jr. (late), Thomas E. Bowman (late), Kenneth A. Christiansen, Bruno Condé (late), Lynn M. Ferguson, Daniel W. Fong, Robert Hershler, Roman Kenk (late), Julian J. Lewis, Jeremy A. Miller, William B. Muchmore, José Palacios-Vargas, William B. Shear, Marc Thibaud, Miloslav Zacharda, and Douglas Zeppelini.

The Cave Conservancy of the Virginias provided a grant to support the preparation of this monograph. We are also indebted to Steven M. Roble for his editorial advice and suggestions which have greatly improved this work. Jerry Lewis provided a thorough and helpful review. Florita Gunasekara and Kristina Hsu assisted with the preparation of the maps. Mike Futtrell of the Virginia Speleological Survey provided numerous cave locations and was essential in resolving discrepancies in reporting cave locations. We also thank the Virginia Speleological Survey for permission to use cave location information in this study. None of this work would have been possible without the help of cavers and cave owners in Virginia. They are the unsung heroes of this study.

LITERATURE CITED

- Aldrich, J. M. 1897. A collection of Diptera from Indiana caves. Annual Report of the Indiana Department of Geology and Natural Resources 21: 186-190.
- Banks, N. 1895. Notes on the Pseudoscorpionida. Journal of the New York Entomological Society 3: 1-13.
- Barber, H. S. 1928. Two new cave beetles related to *Anophthalmus pusio* Horn. Journal of the Washington Academy of Science 18: 195-196.
- Barr, T. C., Jr. 1960. A new genus of cave beetle (Carabidae: Trechini) from southwestern Virginia, with a key to the genera of Trechini of North America north of Mexico. Coleopterists Bulletin 14: 65-70.

- Barr, T. C., Jr. 1965. The *Pseudanophthalmus* of the Appalachian Valley (Coleoptera: Carabidae). American Midland Naturalist 73: 41-72.
- Barr, T. C., Jr. 1981. *Pseudanophthalmus* from Appalachian caves (Coleoptera: Carabidae): the *engelhardti* complex. Brimleyana 5: 37-94.
- Barr, T. C., Jr. 2004. A classification and checklist of the genus *Pseudanophthalmus* Jeannel (Coleoptera: Carabidae: Trechinae). Virginia Museum of Natural History Special Publication No. 11. 52 pp.
- Benedict, E. M., & D. R. Malcolm. 1974. A new cavernicolous species of *Mundochthonius* from the eastern United States (Pseudoscorpionida: Chthoniidae). Journal of Arachnology 2: 1-4.
- Bowman, T. E. 1964. *Antrolana lira*, a new genus and species of troglobitic cirolanid isopod from Madison Cave, Virginia. International Journal of Speleology 1: 229-236.
- Bresson, J. 1955. Aselles de sources et de grottes d'Eurasie et d'Amérique du Nord. Archives de Zoologie Experimentale et Generale 92: 45-77.
- Carpenter, J. H. 1970. *Geocentrophora cavernicola* n. sp. (Turbellaria, Alloecoela) - first cave alloecoel. Transactions of the American Microscopical Society 89: 124-133.
- Causey, N. B. 1959. Some cavernicolous millipeds from the Cumberland Plateau. Journal of the Tennessee Academy of Science 34: 229-237.
- Causey, N. B. 1960. The troglobitic milliped genus *Zygonopus* (Chordeumida, Conotylidae, Trichopetalinae). Journal of the New York Entomological Society 68: 69-80.
- Chamberlin, J. C. 1962. New and little known false scorpions, principally from caves, belonging to the families Chthoniidae and Neobisiidae (Arachnida, Chelonethida). Bulletin of the American Museum of Natural History 123: 303-352.
- Christiansen, K. A. 1960a. The genus *Pseudosinella* (Collembola, Entomobryidae) in caves of the United States. Psyche 67: 1-24.
- Christiansen, K. A. 1960b. The genus *Sinella* Brook (Collembola: Entomobryidae) in Nearctic caves. Annals of the Entomological Society of America 53: 481-491.
- Christiansen, K. A. 1962. Proposition pour la classification des animaux cavernicoles. Spelunca 2: 75-78.
- Christiansen, K. A. 1966. The genus *Arrhopalites* in the United States and Canada. International Journal of Speleology 2: 43-73.
- Christiansen, K. A., & P. Bellinger. 1980. The Collembola of North American North of the Rio Grande. Part 3. Family Entomobryidae. Grinnell College, Grinnell, IA. pp. 637-1042.
- Christiansen, K. A., & P. Bellinger. 1996a. Cave *Pseudosinella* and *Oncopodura* new to science. Journal of Cave and Karst Studies 58: 38-53.
- Christiansen, K. A., & P. Bellinger. 1996b. Cave *Arrhopalites* new to science. Journal of Cave and Karst Studies 58: 168-180.
- Christiansen, K. A., & P. Bellinger. 1998. The Collembola of North America North of the Rio Grande. Revised Edition. Grinnell College, Grinnell, IA. 1,520 pp.
- Condé, B., & C. Bareth. 1996. Une nouvelle espèce de *Litocampa* de grottes de l'état de Virginie (Diplura Campodeidae). Mémoires de Biospéologie 23: 143-147.
- Cook, D. G. 1975. Cave-dwelling aquatic Oligochaeta (Annelida) from the eastern United States. Transactions of the American Microscopical Society 94: 24-37.
- Cope, E. D. 1869. Synopsis of the extinct Mammalia of the cave formations in the United States, with observations on some Myriapoda found in and near the same, and on some extinct mammals of the caves of Anguilla, W. I., and of other localities. Proceedings of the American Philosophical Society 11: 171-192.
- Crabill, R. E. 1952. New cavernicolous *Nampabius* with a key to its northeastern American congeners (Chilopoda, Lithobiidae). Entomological News 63: 203-206.
- Culver D. C., J. R. Holsinger, M. C. Christman, & T. Pipan. 2010. Morphological differences among eyeless amphipods in the genus *Stygobromus* dwelling in different subterranean habitats. Journal of Crustacean Biology 30: 68-74.
- Culver, D. C., J. R. Holsinger, & D. J. Feller. 2012a.

The fauna of seepage springs and other shallow subterranean habitats in the mid-Atlantic Piedmont and Coastal Plain, U.S.A. *Northeastern Naturalist* 19 (Monograph 9): 1-42.

Culver, D. C., P. Trontelj, M. Zagmajster, & T. Pipan. 2012b. Paving the way for standardized and comparable subterranean biodiversity studies. *Subterranean Biology* 10: 43-50.

Delamare Deboutteville, C. 1949. Collemboles cavernicoles du Tennessee et de l'Alabama. *Notes Biospeleologique* 4: 117-124.

Elliott, W. R., & R. W. Strandtmann. 1971. New locality records for *Rhagidia* from Mexican and American caves. *Journal of the Kansas Entomological Society* 44: 468-475.

Estes, J. A., & J. R. Holsinger. 1976. A second troglotic species of the genus *Lirceus* (Isopoda, Asellidae) from southwestern Virginia. *Proceedings of the Biological Society of Washington* 89: 481-490.

Ferguson, L. M. 2009. *Litocampa hoffmani*, a new species of cavernicolous dipluran from southwestern Virginia (Hexapoda: Diplura: Campodeidae). Pp. 301-311 *In* S. M. Roble & J. C. Mitchell (eds.), *A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday*. Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.

Fišer, C., A. Blejec, & P. Trontelj. 2012. Niche-based mechanisms operating within extreme habitats: a case study of subterranean amphipod communities. *Biology Letters* 8: 578-581.

Fong, D. W., D. C. Culver, H. H. Hobbs, III, & T. Pipan. 2007. *The Invertebrate Cave Fauna of West Virginia*. Second Edition. West Virginia Speleological Survey Bulletin No. 16. 163 pp.

Gertsch, W. J. 1984. The spider family Nesticidae (Araneae) in North America, Central America and the West Indies. *Texas Memorial Museum Bulletin* No. 31. 91 pp.

Graening, G. O., D. B. Fenolio, & M. E. Slay. 2011. *Cave Life of Oklahoma and Arkansas*. University of Oklahoma Press, Norman, OK. 226 pp.

Hay, W. P. 1901. Two new subterranean crustaceans from the United States. *Proceedings of the Biological Society of Washington* 14: 179-180.

Hershler, R. 1989. *Holsingeria unthinksensis*, a new genus and species of aquatic cavesnail from eastern North America. *Malacological Review* 22: 93-100.

Hershler, R., J. R. Holsinger, & L. Hubricht. 1990. A revision of the North American freshwater snail genus *Fontigens* (Prosobranchia: Hydrobiidae). *Smithsonian Contributions to Zoology* No. 509. 49 pp.

Holsinger, J. R. 1963. Annotated checklist of the macroscopic troglobites of Virginia with notes on their geographic distribution. *Bulletin of the National Speleological Society* 25: 23-36.

Holsinger, J. R. 1967. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). *United States National Museum Bulletin* No. 259. 176 pp.

Holsinger, J. R. 1969. The systematics of the North American subterranean amphipod genus *Apocrangonyx* (Gammaridae), with remarks on ecology and zoogeography. *American Midland Naturalist* 81: 1-28.

Holsinger, J. R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae), Part II: species of the eastern United States. *Smithsonian Contributions to Zoology* No. 266. 144 pp.

Holsinger, J. R. 2009. Three new species of the subterranean amphipod crustacean genus *Stygobromus* (Crangonyctidae) from the District of Columbia, Maryland, and Virginia. Pp. 261-276 *In* S. M. Roble & J. C. Mitchell (eds.), *A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday*. Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.

Holsinger, J. R., & T. E. Bowman. 1973. A new troglotic isopod of the genus *Lirceus* (Asellidae) from southwestern Virginia, with notes on its ecology and additional cave records for the genus in the Appalachians. *International Journal of Speleology* 5: 261-271.

Holsinger, J. R., & D. C. Culver. 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: zoogeography and ecology. *Brimleyana* 14: 1-162.

- Holsinger, J. R., D. A. Hubbard, Jr., & T. E. Bowman. 1994. Biogeographic and ecological implications of newly discovered populations of the stygobiont isopod crustacean *Antrolana lira* Bowman (Cirolanidae). *Journal of Natural History* 28: 1047-1058.
- Horn, G. H. 1868. Catalogue of Coleoptera from south-west Virginia. *Transactions of the American Entomological Society* 2: 123-41.
- Hubricht, L. 1943. Studies on the Nearctic fresh-water Amphipoda III. Notes on the freshwater amphipods of the eastern United States, with descriptions of ten new species. *American Midland Naturalist* 29: 683-712.
- Hubricht, L. 1963. New species of Hydrobiidae. *Nautilus* 76: 138-140.
- Hubricht, L., & J. G. Mackin. 1940. Descriptions of nine new species of freshwater Amphipoda crustaceans and new localities for other species. *American Midland Naturalist* 23: 187-218.
- Hutchins, B., D. W. Fong, & D. B. Carlini. 2010. Genetic population structure of the Madison Cave isopod, *Antrolana lira* (Cymothoidea: Cirolanidae) in the Shenandoah Valley of the eastern United States. *Journal of Crustacean Biology* 30: 312-322.
- Hyman, L. H. 1945. North American triclads (Turbellaria). XI. New, chiefly cavernicolous, planarians. *American Midland Naturalist* 34: 475-484.
- Ivie, W. 1965. The spiders of the genus *Islandiana* (Linyphiidae, Erigoninae). *American Museum Novitates* 2221: 1-25.
- Jeannel, R. 1931. Campagne spéologique de C. Bolivar et R. Jeannel dans l'Amerique du Nord (1928). 9. Insectes coléoptères et revision des Trechinae de l'Amérique du Nord. *Archives de Zoologie Experimentale et Générale* 71: 403-499.
- Kenk, R. 1977. Freshwater triclads (Turbellaria) of North America. IX. The genus *Sphalloplana*. *Smithsonian Contributions to Zoology* No. 246. 38 pp.
- Keyserling, E. 1886. Die Spinnen Amerikas. Theridiidae. *Nürnberg*, Vol. 2. 295 pp.
- Koenemann, S., & J. R. Holsinger. 2001. Systematics of the North American subterranean amphipod genus *Batrur* (Crangonyctidae). *Beaufortia* 51: 1-56.
- Levi, H. W. 1949. Two new species of cave isopods from Pennsylvania. *Notulae Naturae* 220: 1-6.
- Lewis, J. J. 1980. A comparison of *Pseudobaicalasellus* and *Caecidotea*, with a description of *Caecidotea bowmani*, n. sp. (Crustacea: Isopoda: Asellidae). *Proceedings of the Biological Society of Washington* 93: 314-326.
- Lewis, J. J. 2000. *Caecidotea cumberlandensis*, a new species of troglotic isopod from Virginia, with records of other subterranean *Caecidotea* (Crustacea: Isopoda: Asellidae). *Proceedings of the Biological Society of Washington* 113: 458-464.
- Lewis, J. J. 2009. Three new species of *Caecidotea*, with a synopsis of the asellids of Virginia (Crustacea: Isopoda: Asellidae). Pp. 251-266 *In* S. M. Roble & J. C. Mitchell (eds.), *A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday*. Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.
- Lewis, J. J., T. E. Bowman, & D. J. Feller. 2011. A synopsis of the subterranean asellids of Maryland, U.S.A., with description of *Caecidotea alleghenyensis*, new species (Crustacea: Isopoda: Asellota). *Zootaxa* 2769: 54-64.
- Loomis, H. F. 1939. The millipeds collected in Appalachian caves by Mr. Kenneth Dearolf. *Bulletin of the Museum of Comparative Zoology* 86: 165-193.
- Loomis, H. F. 1943. New cave and epigeal millipeds of the United States, with notes on established species. *Bulletin of the Museum of Comparative Zoology* 92: 373-410.
- Malcolm, D. R., & J. C. Chamberlin. 1961. The pseudoscorpion genus *Kleptochthonius* Chamberlin (Chelonethida, Chthoniidae). *American Museum Novitates* 2063: 1-35.
- Miller, J. A. 2005a. Cave adaptation in the spider genus *Anthrobia* (Araneae, Linyphiidae, Erigoninae). *Zoologica Scripta* 34: 565-592.
- Miller, J. A. 2005b. A redescription of *Porrrhomma cavernicola* Keyserling (Araneae, Linyphiidae) with notes on Appalachian troglodites. *Journal of Arachnology* 33: 426-438.

- Muchmore, W. B. 1967. New cave pseudoscorpions of the genus *Apochthonius* (Arachnida: Chelonethida). *Ohio Journal of Science* 67: 89-95.
- Muchmore, W. B. 1970. New cavernicolous *Kleptochthonius* spp. from Virginia (Arachnida, Pseudoscorpionida, Chthoniidae). *Entomological News* 81: 210-212.
- Muchmore, W. B. 1973. The genus *Chitrella* in America (Pseudoscorpionida, Syarinidae). *Journal of the New York Entomological Society* 81: 183-192.
- Muchmore, W. B. 1974. New cavernicolous species of *Kleptochthonius* from Virginia and West Virginia. *Entomological News* 85: 81-84.
- Muchmore, W. B. 1976. New cavernicolous species of *Kleptochthonius* and recognition of a new species group within the genus (Pseudoscorpionida: Chthoniidae). *Entomological News* 87: 211-217.
- Niemiller, M. L., & K. S. Zigler. 2013. Patterns of cave biodiversity and endemism in the Appalachians and Interior Plateau of Tennessee, USA. *PloS One* 8: e64177.
- Packard, A. S. 1881. In E. D. Cope & A. S. Packard. *Fauna of the Luray and New Market caves, Virginia*. *American Naturalist* 15: 231-232.
- Packard, A. S. 1884. New cave arachnids. *American Naturalist* 18: 202-204.
- Packard, A. S. 1888. The cave fauna of North America with remarks on the anatomy of the brain and origin of the blind species. *Memoirs of the National Academy of Sciences* 4: 1-156.
- Palacios-Vargas, J. G., & J. C. S. Benito. 2007. A new genus and three new species of Neanuridae (Collembola) from North America. *Journal of Cave and Karst Studies* 69: 318-325.
- Paquin, P., & N. Dupérré. 2003. Guide d'identification des Araignées (Araneae) du Québec. *Fabriques, Supplément* 11: 1-251.
- Paquin, P., N. Dupérré, D. J. Buckle, & J. J. Lewis. 2009. *Oreonetides beattyi*, a new troglobitic spider (Araneae: Linyphiidae) from eastern North America, and re-description of *Oreonetides flavus*. *Journal of Cave and Karst Studies* 71: 2-15.
- Park, O. 1956. New or little known species of pselaphid beetles from southeastern United States. *Journal of the Tennessee Academy of Science* 31: 54-100.
- Petrunkévitch, A. 1925. Descriptions of new or inadequately known American spiders. *Annals of the Entomological Society of America* 18: 313-323.
- Pipan, T., & D. C. Culver. 2005. Estimating biodiversity in the epikarstic zone of a West Virginia cave. *Journal of Cave and Karst Studies* 67: 103-109.
- Pipan, T., & D. C. Culver. 2012. Convergence and divergence in the subterranean realm: a reassessment. *Biological Journal of the Linnean Society* 107: 1-14.
- Schiner, J. G. 1852. Fauna der Adelsberger-, Luegger-, and Magdalenen Grotte. Pp. 231-271 In A. Schmidl (ed.), *Die Grotten und Höhlen von Adelsberg, Lueg, Planina und Laas*. Braunmüller, Vienna, Austria.
- Schneider, K., & D. C. Culver. 2004. Estimating subterranean species richness using intensive sampling and rarefaction curves in a high density cave region in West Virginia. *Journal of Cave and Karst Studies* 66: 39-45.
- Schultz, G. A. 1970. Descriptions of new subspecies of *Ligidium elrodii* (Packard) comb. nov. with notes on other isopod crustaceans in North America (Oniscoidea). *American Midland Naturalist* 84: 36-45.
- Schwank, P. 1986. Microturbellaria from subterranean freshwater habitats. Pp. 47-56 In L. Botosaneanu (ed.), *Stygofauna Mundi*. E.J. Brill, Leiden, The Netherlands.
- Shear, W. A. 1972. Studies in the milliped order Chordeumida (Diplopoda): a revision of the family Cleidogonidae and a reclassification of the order Chordeumida in the New World. *Bulletin of the Museum of Comparative Zoology* 144: 151-352.
- Shear, W. A. 2010. The milliped family Trichopetalidae, part 2: the genera *Trichopetalum*, *Zygonopus* and *Scoterpes* (Diplopoda: Chordeumatida, Cleidogonoidea). *Zootaxa* 2385: 1-62.
- Shear, W. A. 2011. Cave millipeds of the United States. X. New species and records of the genus *Pseudotremia* Cope. 2. Species from Virginia, USA (Diplopoda, Chordeumatida, Cleidogonidae). *Zootaxa* 3109: 1-38.

- Shear, W. A., & D. A. Hubbard, Jr. 1998. New milliped records for Virginia and Georgia: *Ameractis satis* (Zosteractinidae, Julida, Diplopoda). *Banisteria* 12: 41-42.
- Shoemaker, C. R. 1940. Notes on the amphipod *Gammarus minus* Say and description of a new variety, *Gammarus minus* var. *tenuipes*. *Journal of the Washington Academy of Science* 30: 388-391.
- Sket, B. 2008. Can we agree on an ecological classification of subterranean animals? *Journal of Natural History* 42: 1549-1563.
- Steeves, H. R., III. 1963. Two new troglobitic asellids from West Virginia. *American Midland Naturalist* 70: 462-465.
- Steeves, H. R., III, & J. R. Holsinger. 1968. Biology of three new species of troglobitic asellids from Tennessee. *American Midland Naturalist* 80: 75-83.
- Tellkamp, T. A. 1844. Beschreibung einiger neuer in der Mammuth-Hohle in Kentucky aufgefundenen Gattungen von Gliederthieren. *Müllers Archiv Anatomie und Physiologie* 4: 308-312.
- Thibaud, J.M. 1995. Une nouvelle espece d'*Schaefferia* d'un grotte des Etats Unis d'Amerique (Collembola, Hypogastruridae). *Revue Francaise d'Entomologie* 17: 77-78.
- Thibaud, J. M. 1996. Une nouvelle espece d'*Typhlogastrura* de deux grottes des Etats Unis d'Amerique (Collembola, Hypogastruridae). *Revue Francaise d'Entomologie* 18: 11-12.
- Valentine, J. M. 1931. New cavernicole Carabidae of the subfamily Trechinae Jeannel. *Journal of the Elisha Mitchell Scientific Society* 46: 247-258.
- Valentine, J. M. 1932. *Horologion*, a new genus of cave beetles. *Annals of the Entomological Society of America* 25: 1-9.
- Valentine, J. M. 1937. Anophthalmid beetles (fam. Carabidae) from Tennessee caves. *Journal of the Elisha Mitchell Scientific Society* 53: 93-100.
- Valentine, J. M. 1945. Speciation and riation in *Pseudanophthalmus* (cavernicolous Carabidae). *Transactions of the Connecticut Academy of Arts and Sciences* 36: 631-672.
- Valentine, J. M. 1948. New anophthalmid beetles from the Appalachian region. *Geological Survey of Alabama Museum Papers* 27: 1-20.
- Vandel, A. 1950. Campagne spéléologique do Bolivar et R. Jeannel dans l'Amérique du Nord (1928). Isopodes terrestres recueillis par C. Bolivar et R. Jeannel (1928) et le Dr. Henrot (1946). *Archives de Zoologie Experimentale et Generale* 87: 183-210.
- Vandel, A. 1965. Les Trichoniscidae cavernicoles (Isopoda terrestria; Crustacea) de l'Amerique du Nord. *Annales de Spéléologie* 20: 347-389.
- Walker, B. 1925. New species of fresh-water operculates. *Nautilus* 39: 5-8.
- Wray, D. L. 1952. Some new North American Collembola. *Bulletin of the Brooklyn Entomological Society* 47: 95-106.
- Zacharda, M. 1980. Soil mites of the family Rhagidiidae (Actinedida: Euopdoidea). *Acta Universitatis Carolinae – Biologica* 1978: 489-795.
- Zacharda, M. 1985. New Rhagidiidae (Acarina: Prostigmata) from caves of the U.S.A. *Věstník Československé Společnosti Zoologické* 49: 67-80.
- Zacharda, M., D. Fong, H. H. Hobbs III, E. Piva, M. E. Slay, & S. J. Taylor. 2010. A review of the genus *Traegardhia* (Acari, Prostigmata, Rhagidiidae) with descriptions of new species and a key to species. *Zootaxa* 2474: 1-64.
- Zagmajster, M., D. C. Culver, M. C. Christman, & B. Sket. 2010. Evaluating the sampling bias in pattern of subterranean species richness – combining approaches. *Biodiversity and Conservation* 19: 3035-3048.
- Zeppelini, D., & K. A. Christiansen. 2003. *Arrhopalites* (Collembola: Arrhopalitidae) in United States caves with the description of seven new species. *Journal of Cave and Karst Studies* 65: 36-42.